Front cover: *Campanula tommasiniana*. Painting by Paul Bowden.

Back cover: Artist at the rock garden, Hay Estate, Newbury, New Hampshire. Photograph by Dianne Huling.

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From the Editor

If there is one thing that our Society does better than any other garden group in North America, surely it is the annual Seed Exchange, the product of efforts by many people in several chapters each year. Instructions for participating are being mailed with this issue. If we are to maintain NARGS as a vital organization, we need to encourage members and potential members to recognize the benefits of growing plants from seed. And that is the goal of this issue of our magazine.

I've grown thousands of species from seed (no, I don't still have all of them!), and this has made it feasible for me to stock a large country garden that could not have been filled economically with purchased plants. Moreover, in this way I've been able to build up a systematic collection of more than 1300 bulbous species, the majority of which never appear in commercial catalogs. Once you're hooked on a particular plant family or genus, you almost have to turn to raising plants from seed. Even trees: last summer an oak specialist in Germany asked me to send acorns from one of our local native species for propagation in his arboretum.

On average, about one-fifth of the Society's members donate to the Seed Exchange, and about one-third of members request seeds. Both these percentages should be higher. Donating as few as five items will bring you a "donor's share" of ten extra packets in exchange. Kristl Walek's authoritative article in this issue will help you get started collecting donations from your own garden or nearby natural areas.

Remember that collecting seeds may be prohibited in certain categories of state and federal lands unless you obtain a permit. Rare and endangered plants present a particular ethical problem in terms of seed collection, addressed in this issue by David Rankin.

In addition to NARGS, the Alpine Garden Society and Scottish Rock Garden Club (see our advertising section) operate exchanges, as do many specialist plant societies. Seed sellers can be found on the Internet, and some advertise in this magazine, usually in the fall and winter issues when the new crop is available. They may produce glossy catalogs or simple lists with or without descriptions—and the latter are often the real gem mines.

And why not use this inexpensive means to begin propagating your own plants? Carlo Balistrieri's introductory article will help any beginner. For those seeking greater challenges, this issue offers hints on seed propagation of gesneriads (by Tony Reznicek) and castillejas (Dave Nelson and David Joyner). Inexpensive supplies and a good fund of patience and care will eventually bring you a garden like no other.
Seed Sowing Basics

Carlo A. Balistrieri

Sowing seeds is one of those mystical, magical activities many of us engage in as children and then let fall by the wayside in favor of more “adult” occupations. Shame, shame, shame! Arise, rock gardeners! Become like a child again!

Nothing brings back the halcyon days of childhood like taking a germ of plant life, though it doesn’t even look alive, and nurturing it to flower. From dust to corn-kernel-sized, seeds of rock garden plants are often the best way to amass a collection of choice material for our stony haunts. Collected personally, obtained through seed exchanges, or purchased from vendors, seeds are windows on the world of rock garden plants.

Getting Ready

A little organization will greatly increase the enjoyment you get out of raising plants from seed. Getting things ready before you sow is one of the key activities to speed you on your way—and help avoid frustration. Gathering materials and information will make things go more smoothly and quickly.

First, concentrate on getting your seeds in one place and finding the information necessary to sow them properly. Seeds come from many sources, including our own gardens. Read about them elsewhere in this issue of the Quarterly.

Information about germination requirements also comes from many sources. Often the catalogues we order from, or the seed packets in which the seeds are delivered, will indicate if some special treatment is necessary. Books are another fine source of detailed information. Websites contain data on hundreds of species of rock garden plants, and Internet discussion groups often suggest methods for germinating seeds. Making a list of all the seeds you’re sowing along with the method you’ll use for each is the first step in record-keeping (see below).

You’ll eliminate many stops and starts in the process if you round up all the supplies you’ll need before you start. Clean pots, flats, or liner trays should be on hand. All the components of your potting mix, your mulch, tools, and water should be ready to go. Don’t forget labels, pencils, and anything that will be
Record Keeping

Record keeping is a must in seed sowing. Unless you're tripping through your garden at the end of the year broadcasting seeds in all directions like a modern-day Demeter, you've likely already started the process by cleaning the seeds you collected and putting them into envelopes, with names and dates of collection.

Since you've already got all your seeds together and have researched the method you will use to sow each kind, putting together a simple spreadsheet (on the computer if you know how; otherwise, a sheet of paper will do) is easy. It should include columns for the names of the plants and sources of the seeds, along with sowing technique (cold treatment, warm, warm with light, pre-soak, scarify, etc.). More columns should be available for the dates of sowing, first germination, potting on, and planting out. A notes column at the end can hold any other useful information you'd like to record.

Just a hint on plant names: do not plant your seeds or offer them to an exchange with a cultivar name (the names, usually in English, that appear in single quotation marks after the botanical name). Selected varieties will set seed, but the resulting progeny will vary and not come true. A cultivar should only be propagated vegetatively if you want to keep the name. Write *Ramonda myconi* ex 'Rosea' on the seed tag; "ex," Latin for "from," indicates that the seed sown is from one of the pink cultivars. You will get pink-flowering plants along with others, but none can properly be called 'Rosea'.

The Elements of the Process

Once all your seeds are entered into the spreadsheet, you can begin to sow. It's best to dedicate a work space to this endeavor. For me the process extends over a period of weeks, and constantly cleaning up, putting away, and starting over would drive me to the nearest nursery to buy plants and pitch the whole idea of seed growing. Putting all your materials within arm's length in some sort of order (whatever works best for you) eliminates much back and forth. It also localizes the effort and makes it nearly impossible to lose anything you need.

In broad terms, I divide the seeds I sow into warm germinators and those requiring "stratification," or cold treatment. As I sow, I have two flats nearby; one to carry those warm germinators to their position under lights, the other for seeds to be stratified, which will sit on the floor for a couple of weeks to allow them to take in water before being put outdoors for a couple of months of winter chill.
The Mix

Everyone wants a precise recipe for a seed-sowing medium. Trust me, you can find dozens. My advice: keep it simple and convenient. I keep various components for potting mixes on hand and concoct my media as I go along.

In general, the mix I use is composed of commercial soilless potting mix, crushed granite, and horticultural grade perlite, in just about equal parts. The key is to create a free-draining yet moisture-retentive mix. Since I often don’t remove seedlings from their seed pots for some time, my mix approaches the same one I use as a general potting mix.

The soilless component I use at present is Metro-Mix® 510. It exhibits good air porosity (the fluff factor) and water retention. Some people may consider 510 a bit coarse for a seedling mix, but this product also forms the base for my potting mix, I’ve got experience with it, and for consistency and simplicity’s sake, I’m sticking with it until I come up with something better. There are many other products that work equally well. Use what is easy for you to find and affordable.

Crushed granite is most easily found as poultry grit at farm supply stores or feed mills. Even New York City residents can find such outlets within an hour or so of the city center. Any gravel that is chemically inert can be used. I prefer a size approaching that of aquarium gravel. Again, the watchword is convenience. The function of grit is to keep the soilless part of the mix from compacting and eliminating the air spaces so necessary for good root health.

Perlite performs much the same function but is lightweight. It’s an expanded volcanic product—the little white blobs that float out of the pot when you water. Since it’s porous, it helps keep air available. It’s also great for rooting cuttings.

You’ll begin to recognize the “look” of a good mix after you’ve got some experience putting them together. Pick up a handful of slightly moist medium and squeeze it like a snowball. When you open your hands, it should fall apart. If not, you need more gravel/perlite.

I vary the amount of each component based on the seeds that are being sown. Alpine and rock garden plants go into a mix that is heavy on inorganic matter, mostly grit. Woodland plant seeds go into a mix that’s around half-and-half. They usually require more moisture retention, but I still want the mix to drain.

Other components of a seed mix can include crushed oyster shell and milled sphagnum moss. These are sometimes used to address particular needs of special plants. Plants from areas with limestone-based soils will appreciate the calcium that is slowly released by crushed oyster shell. Working a small helping of this mineral-rich substance into your mix provides it. Crushed oyster shell is available wherever crushed granite is found. It is sometimes called “poultry shell.” Another lime product is “prilled,” or slow-release, dolomitic lime, used to raise the pH of garden soils, particularly on lawns.

The antifungal properties of sphagnum moss are used to advantage by growers concerned that plants will succumb to “damping off” as seedlings. Milled sphagnum (not sphagnum peat, but the fresh moss itself) is finely ground and can be used as a top-dressing on seed pots to prevent this fatal fungal condition.
It is not a required step, but it reassures some growers. Careful watering achieves much the same end. If you use milled sphagnum, it is advisable to wear gloves and avoid breathing the dust from the product.

**The Container**

Clay or plastic? The debate has raged for years. For all practical purposes, the argument is over. Regardless of what you choose as a receptacle for your adult plants, nearly everyone sowing seed does it in plastic pots. They are cheap, light, uniform, and easy to clean. Seeds can also be sown in flats, trays, and plug liners (trays with rows of individual depressions). Some seed fares better sown directly into the garden. Your choice of container affects your care of the seed. Clay "breathes" and dries out more quickly than plastic, which holds moisture for a longer time. Adjust watering accordingly.

**Mulch**

Many growers top-dress their seed pots with a layer of grit. This has a number of benefits. It keeps seeds in the soil and prevents splashing water from blasting them out of the pot. It shades the surface of the potting mix and helps to keep it moist. The weeds that will inevitably pop up are easier to remove, and it cuts down on the formation of algae, moss, and liverwort. I use the same grit that goes into the mix.

Your research will reveal that certain seeds must be exposed to light to germinate. The grit layer must be much thinner, or skipped altogether on these pots.

**Sowing Your Seeds**

Those accustomed to "sowing their wild oats" will find this process a bit different. Theoretically, seeds can be sown at any time if you give them the conditions they need to overcome germination inhibitors. In the spirit of keeping things simple, aftercare of the resulting plants should be considered, and that's why I sow in winter.

Seeds from the previous year are harvested at the end of the season. They generally get to the exchanges in fall. The exchanges (and seed companies) send out their eagerly awaited lists after they've catalogued the harvest, and this means those publications are the finest of our holiday presents. Seed nuts pull all-nighters to make their selections, returning their picks the very next day. Early the following year, our precious cargo arrives.

For rock gardeners, the arrival of seeds in the dead of winter is perfect timing. Not only is the act of seed sowing a restorative therapy at this time of year, it's
perfect if you consider the needs of the plants. Warm-growing plants will have a chance to germinate and gain some much-needed mass before being gradually exposed to outdoor conditions when the weather warms. Seeds with chilling requirements have them easily met by being placed outdoors, a couple of weeks after sowing, to endure the rest of the winter in the same manner as their cousins in the wild.

I sow between New Year’s and Valentine’s Day (except for those seeds that must be sown fresh, which I sow as soon as I get them).

Here’s How

Fill a flat with pots and fill the pots with your mix, tamping it down lightly to about the collar of the pot. Thoroughly moisten all the pots, making sure that you can see water coming from the drain holes. Alternatively, set it in a tub of water until the surface appears wet. The flat will be appreciably heavier when you move it back to your potting bench or table. (Photos, p. 250.)

Create the label for each pot before you open the seed packet. For extra security, write the name of the plant or a code on the side of the pot itself.

Make sure your hands are now clean and dry. Carefully tear open the seed envelope and dump its contents into your palm. For small seeds, take a pinch between your a thumb and forefinger and sprinkle them over the moistened surface of the pot. Don’t sow too thickly, or you’ll have problems later on. If necessary, sow more than one pot or save extra seeds for trading or sowing next year. Larger seeds can be spaced and placed individually, then pressed into the surface of the mix until flush.

I’ve started planting bulb seeds deeper (filling the pot halfway, sowing, then filling the pot as above) at the suggestion of veteran seed-sowers “across the pond” who feel it gives the young plants an advantage. This is so because many monocots are “hypogeal” germinators which form a radicle (first root) before the cotyledon (seed leaf) emerges; if the seeds are too close to the surface, the radicle will push the seed well above the soil, often resulting in failure.

If the plant requires light to germinate, a very thin coat of grit (or none at all) can be applied. If not, fill the remainder of the pot with a layer of grit (about a quarter-inch, or 1 cm) and set the pots in the appropriate “cool” or “warm” flat.

When the flat is filled, give it a light watering, using a watering can with a very fine “rose” or a mist nozzle, to wet the surface and bond the seed to the potting mix. Then set your warm-germinating flat under lights or in a heated greenhouse, and your cold treatment flat in a cool spot.

Treatment of Seeds

The most common extra treatment you’ll run into, besides those that need to freeze their little seed coats off, is scarification for seed with impervious seed
coats. Some hard-coated seeds are not able to take in water without a break in the coat. In nature this occurs with the grinding action of soil. In the cushy confines of cultivation, we need to help things along.

Scarification (don’t confuse it with stratification) can be accomplished in several ways. In the case of large seeds, the coats can be nicked with a sharp blade, such as a small mat knife. Large and medium-sized seeds can also be rubbed gently between two pieces of sandpaper. Both methods can lead to bloodied fingertips, though, and neither is suitable for small seeds.

A solution for all impervious seeds is to get a small, clean container (a film canister will do) with a tight-fitting lid. Fill it one-third or so with coarse sand and then put in your seed and securely cap the container. Now shake it like you’re in a mariachi band. Whether you see it or not, the seed coats will be compromised enough to take in water. When done, use the container to distribute its contents, seed and sand, into the pot. Cover with grit and place with its like-temperature friends.

Some especially hard-coated seed is scarified by pouring nearly boiling water over it. Like nicking the coats with a blade, this breaches the surface of the seed, allowing it to begin taking in water to start the process of germination.

Another pre-sowing technique that is beneficial to many seeds, and necessary for some, is a soak. Easily accomplished, a pre-sowing soak jump-starts many seeds. Simply put seeds of the plants that need it into small containers of water with a drop or two of plain dishwashing liquid. If the water discolors after a time, rinse with clear water. Usually a 24- to 48-hour soak is sufficient; then plant as usual.

Lights

The most common mistake made when sowing seed, whether of rock garden plants or vegetables, is insufficient light. Although nearly any light will do, not getting enough of it will cause plants to etiolate, or stretch out reaching for more. Growth becomes lopsided and soft, and it’s often hard for the plant to recover.

Fluorescent fixtures are the cheapest and most easily available light source. They are sold as “shop lights” and commonly found in 4-foot lengths. There are many bulbs available, some with special wavelengths for use with plants. Cool-white bulbs, the cheapest variety, work just fine, although many growers prefer a mix of cool white and grow lights in their fixtures. The key is to keep lights close to the seed pots (and the plants as they grow). Aim for 6 to 10 inches (15–25 cm) from the tops of the pots. This will keep seedling growth compact and sturdy.

Afterthoughts

Now that everything is done and your pots are under lights, relax. It’s a proven fact that checking your seed pots every 5 minutes does not make seeds germi-
nate faster. Check once a day and record each new arrival in your spreadsheet with its date of germination.

Keep the pots moist, but not sopping wet. Algae or moss growth is a sign of over-watering. Fertilizer will not be necessary until the seedlings are well along. Nutrients in your potting mix will hold them until then. Fertilizing too early will burn sensitive young growth.

Some seeds will germinate within a matter of days, others in weeks; and within the first three months, most of the warm germinators should be showing results. Do not be in a hurry to dump out pots that appear empty. Some seeds take years to germinate, and others are just erratic and slow. A third group completes the first part of its growth underground and won't show a leaf until the second season. Find an out-of-the-way place outdoors to set these pots until you're relatively certain that they are well past hoping for.

When, as will certainly be the case, your pots are full of cheerful little seedlings, it's time for the brutal task of dumping them out, teasing them apart and potting them on. Prepare individual pots in advance, watering the flat ahead of time as above. This is important for two reasons. First, it is easier to make an opening in the mix with a chopstick or other implement if the mix is moist. Second, a moist substrate allows you a period of days when you don't have to water the newly potted plants. This means the seedling can take hold and establish itself before any additional water is applied. This is a big help in the battle against fungal and other seedling diseases.

Now ease the contents of the seed pot onto your working space. Rather than pulling all the seedlings apart right away, try to keep the potting mix intact. Working from an edge, tease out the seedlings one at a time and transfer them immediately into the prepared individual pots. Firm them in carefully and set them back under the lights when you've filled your flats.

When the weather allows, move your seedlings gradually into the great outdoors. Hardening them off is an important step toward getting them ready for the garden. Expose them to sun, wind, and shifting temperatures slowly by putting a light cover over them for the first few days.

Congratulations! You've done it—and your garden will never be the same. The unending variety of garden-worthy plants is yours. The variation of species, and within species, that you can achieve with seed is unparalleled by anything you can purchase. Plants will be available to you in numbers to help avoid the "Noah's Ark" condition that afflicts most plant collectors. Seed sowing can be a solitary, meditative activity, or an occasion for a party. Whatever your course of action, sow a seed.

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On the wall of my seed company office is a framed reminder:

If there is no seed in the receptacle, don’t collect it . . .
If there is only chaff in the bag, don’t clean it . . .
If the seed does not contain an embryo, don’t save it . . .

And next to this is another:

Strive to know the plants by their seed . . .

Seed Production: In House

I live on the same property where I run my business—eight acres in farm country in the Ottawa Valley of Ontario, Canada. Approximately six acres are devoted to seed production.

I formerly grew the plants in rows in seed production areas. However, I abandoned this practice over time due to the risks involved in having all seed stock growing together in one area. The potential dangers from weather, insects, disease, or wild animals are too great if your entire inventory is grown in close quarters. I experienced this at first hand during an ice storm in 1998, which wiped out the seed-production areas.

The plants from which seed is collected are now found within the landscaped structure of the garden, grown en masse. Depending on how much seed is required, I grow from one to 100 plants of any particular species. This method also provides a healthier environment for pollinators, and, as a result, better-quality seed.

The original stock plants are grown from wild-collected seed whenever possible, and new genetic stock is introduced regularly. Care is taken to separate the notorious “crossers,” but otherwise plants are open-pollinated, as is the standard practice in the seed business.
Seed Production: In the Wild

Whenever possible, seed is collected from wild sources. While I sometimes travel great distances for seed collection, most years my energies are spent within a 100-km radius of home. On average, I spend three to five days per week in the wild; the remaining two days I harvest from the garden. Collecting begins in early June, accelerates as the season progresses, and normally does not stop until sometime in December for the very late-ripening (usually woody) species.

I also custom-collect for other seed houses and have standing orders from nurseries propagating native plants. One large batch of *Asarum canadense* seed might take two or three days of solid picking in the woods (at ground level, at the beginning peak time for mosquitoes and black flies) and a solid week to clean the seed.

I collect herbaceous and woody species as well as fern spores in very diverse habitats from bogs to alvar, meadow, and woodland. (Alvars, unique landscapes that occur only in the eastern European Baltic region and the Great Lakes Basin of North America, are grassland, savanna and sparsely vegetated rock barrens that develop on flat limestone bedrock with shallow soils.) It is not the romantic stereotype often put forward; but to those of us who love this life, there is nothing better than heading out again and again with our backpacks ready to be filled.

The threshold difficulty with wild collecting in a developed world is in finding the actual wild spaces. In our area, this is often private land. Luckily, many landowners here still own large acreages (100 acres being common), often with relatively undisturbed ecosystems. Over the past 17 years I have built up a strong resource of seed-collecting spots, but each year I lose at least one favorite site as the bulldozers move in to create yet more civilization.

A second challenge is the perpetual search for the "seed mother lode." This is finding spots where particular species are abundant—both a practical and an ethical necessity. It is an important consideration for me not to seriously impact any particular site in terms of how much seed is collected there. Also, I would prefer to collect all the seed I require in one area, rather than spending the day driving from one spot to another accumulating seed of the same species.

Once I've found the perfect collection spot, I need to get there at the right time. The timing of seed ripening and collection is relatively easy in the garden: one simply walks around and sees what is ready. But this is a bit more complex in the wild, especially if you have to drive some distance. Over the years I've made charts of wild collecting spots and harvesting times so I can see at a glance what is coming up for collection, and where. Notwithstanding changes in weather conditions, the time of seed ripening has been amazingly consistent; within one week each year. Luckily, few species are so unforgiving that they must be collected within a very narrow time frame. A species needs to ensure its survival, so its seed is rarely dispersed all at once.

No matter where one collects the seed, a preliminary evaluation should be made of whether there is in fact any seed worthy of collection. How does one
know? Some of this is obvious: Is the seed receptacle empty? Is it insect-infested, deformed, or damaged? Is the seed plump so as to indicate the presence of an embryo? If the seed is large enough, one can make some of these threshold judgments in the field with the naked eye. If I am certain the seed is no good, I do not bother to collect. Ultimately, I do not trust my eye with any seed. As I have learned too often, the only way to know whether a seed is good in the end is to test it by subjecting it to moisture.

Seed Collection

Harvesting seed is low-tech. All seed is hand-collected in bags—paper for species that shed dry from the plant, plastic for species producing berries or fruit. The dry seed is further dried either inside the paper bags or on trays. These are simply left in the greenhouse on the benches until the seed is ready to be cleaned. The seed in fruit or berries is kept in the Ziploc bags until cleaned. Fern spores are collected by harvesting the fronds of the plants (the entire leaves) in oversized paper bags.

Equipment that always comes with me on wild excursions, in addition to the obvious bags, includes gloves, moist towelettes (for handling poisonous seed and cleaning sticky hands), a hammer, a Swiss Army knife, and a "tree-seed picker" (a painter's extension pole with the metal portion of a paint roller bent into a hook shape screwed into the end, affectionately named "Le Hook"). The last is used to bend down very high branches in order to get at the seed. Sometimes I take knee pads if I expect to be down on all fours for the entire day.

Dry seed is ripe when it naturally "wants to hit the ground," when the wind starts taking it away or the wildlife claims it. Seed receptacles will often change color or open to release the seed. Recognizing when seed is ripe is an intuitive, learned, experiential skill. Everyone can understand ripe poppy seeds spilling from the holes in their seed capsules, but some plants are not so straightforward. Although I have collected seed for over 20 years, it took two seasons to understand when to collect *Erythronium americanum* seed. This I now know is harvested when the underdeveloped-looking soft, beige pods lie on the ground, their stalks often still attached to the remains of the plant. If the seed is collected then, before it is reclaimed by wildlife, it will finish ripening left in its pod in the humid environment of open plastic bags, just as it would lying on the moist ground in the woods. One can observe the seed harden and change color to brown. It is then that it is cleaned of the remaining slimy debris, and moist-packed immediately to preserve viability. *Galanthus* species can be handled in a similar manner, even while the pods are still slightly green, and ripened inside a plastic bag.

*Dirca palustris* (leatherwood, a shrub) was another species that took a number of seasons to learn to collect. This is one of the very few species we must watch carefully each year, as the seed can be lost to the forest floor within a 48-hour period. Once it is ready to expel from the seed capsule, it does not wait for me to arrive. And even when I catch the seed at the right moment, a high percentage of the seed will be empty, so I must hand-sort—a laborious and time-consuming process.
While a “ripe” color of the seed is often a good clue (the norm being brown to black, or brightly colored, soft berries in the case of fruits), some seed is naturally shed “green” or unripe-looking, such as the seed of sweet fern (Comptonia peregrina, not actually a fern). The herbaceous Knautia macedonica is also collected at the greenish or light-beige phase. Natural dropping of the seed, not color, is the deciding factor here.

Fern spores follow the same rule, shedding rather than color being the deciding factor. The spores form in the back of the leaf, or on a separate fertile, spore-bearing frond in the center of the plant. The spores are gathered together in clusters called sori and covered with a membrane called an indusium, which lifts up when the spores are ripe. Spores can be yellow, green, brown, or black. As a very general rule, green spores are often ephemeral (of brief viability in storage).

The best rule of thumb for timing spore collection is an intuitive one. You touch the spore sack. If your hand gets covered with what feels like a smooth dusting of talcum powder, your timing is likely correct, even if the color or the general appearance of the sori looks wrong. Until I taught myself the “talcum-powder” lesson, I was often wrong, relying too much on the visual appearance of the spores. Often when the spore sack is quite brown and lifted up, the spores have already been released. The spore-bearing fronds are gathered in large envelopes, stood up on end in a warm place to dry, and allowed to release the spores, which will “waft” off like dust. I have been in the woods on a peak spore-release day for a particular species and, in the right light; could literally see clouds of spore releasing into the wind.

While I collect seed in many environments, collecting tree seed ranks high on my list of pleasurable activities, as this is often done in the forest, where I feel particularly happy and comfortable. Trees produce seed in a more interesting variety of receptacles than herbaceous plants do, and this too fascinates me. Among them are cones, pods, berries, fruits, nuts, wings, and acorns. For genetic diversity, I try to collect tree species from various sites (more northerly spots for hardiness), and from different individual trees. I choose the healthiest, most productive specimens.

Before I begin, I ensure that I am collecting good seed. First, look for tell-tale holes or spots that could indicate insect damage. Also, avoid taking “suspect” seeds—any that are obviously distorted or undeveloped.

Many tree seeds are bulky; Quercus (oak), Juglans (black walnut, butternut), Fagus (beech), Gymnocladus dioicus (Kentucky coffee tree), and Carya (hickory) usually contain one seed per receptacle. Before gathering these heavy seeds, crack the shell or cut through a few of the fruits, if possible, to ensure they actually have seed inside and that the seed is not infested by insects. Live, healthy seeds will be white or green and noticeably plump. I always carry a small hammer to crack open these seeds and inspect them before collection. Oak, Tilia (linden), and Acer (maple) seeds are often empty or infested. Checking before the seed becomes dry and hardens is easy and can be done with fingernail, penknife or your shoe on the spot.

Collecting woody plants’ seed at the right time is again very important, as underripe seed will mean an immature embryo and overripe seed may be rotten or
damaged by insects. While keen observation of individual species is the best gauge of seed readiness, one can use the following rough guidelines for woody species:

Color. As seeds ripen their receptacles normally change color, starting out green and turning tan, brown, gray, or yellow. Ripe conifer cones may still appear green, but their scales will be edged brown. They are ideally picked when tan, but before they open and release their seeds. Open cones found on the ground will be largely empty. Fruits will take on their ripe colors of red, orange, blue, or black and may become juicy and soft. Winged fruits, pods, and cones will also lighten and become less dense as they ripen and dry.

Opening or dropping. With ripeness, the seed receptacles may split open, fall off the plant, or be carried away by the wind. This is a sure sign that the seed is ready. It seems trite to say, but wildlife also waits for seed to ripen and will begin to harvest seeds as soon as they are ready, so if you are unsure, watch the creatures, because they know.

While there is always a small risk of missing a harvest, there is total waste in collecting unripe or underdeveloped seed. Without a fully developed embryo the seed is simply compost. My long experience with seed exchanges has taught me that most inexperienced seed collectors make the mistake of harvesting too early, and “empty” or improperly developed seeds are regularly submitted to exchanges.

Seed Cleaning

It needs to be said that seed cleaning has nothing to do with viability. While seed houses are held to a certain standard, and some seed debris may contain insects, home growers or nursery persons collecting seed for their own propagation need not (with one exception) clean it. Any debris remaining in a seed lot will be attacked by fungi as it breaks down in moisture. However, the fungi will not attack live, healthy seed, which will germinate notwithstanding any fungus attack to the chaff. This is very different from fungi attacking the actual seed (which is normally a symptom of weak, dead seed, or seed lacking an embryo, making it in effect chaff).

What should always be cleaned is seed contained in fruit. This is because the fruit is believed to contain germination inhibitors that prevent the seed from germinating while still contained in the fruit. In nature the cleaning function is normally performed by animals or by the elements washing the seed.

Most dry seed can be safely left in its collection bags until there is time to clean it, even if that is months down the line. This after-drying is often required in any event for many dry-stored species, and some species will not germinate if sown too soon after harvest. The after-drying requirement can be as little as a few days or months or as long as a year (e.g., many Opuntia species). Such seed will also alter its germination pattern after dry storage, so older seed is often rotated here with fresh seed, which is kept for the following season.

Whenever there is uncertainty about whether a batch of seed is good, the cleaning is left until after testing. A small pinch of the uncleaned seed is placed
into a Petri dish on moistened filter paper and placed in warmth. Regardless of
the germination pattern of the seed (whether it is a warm or cold germinator or
requires some other treatment), the seed will show you its health when exposed
to moisture. If it rots or gets attacked by fungi (which will not harm a healthy
seed), it is composted. If the seed stays sound (healthy-looking and firm) it is
fine, whether it germinates in this preliminary test or not.

Seeds that tolerate dry storage are normally cleaned by sifting, blowing, tossing,
or rubbing, or a combination of all these. The tools of my trade are sieves and
bowls of every size and shape. I do not recommend plastic sieves. My favorite
bowl is a particular antique wooden one—just the right size and outward angle
for seeds, and no static, which is a real problem with plastic, metal, and glass.
This bowl gets used for tossing the seed. Once you master the art, the chaff will
land on one side, the clean seed on the other. Seed without embryos will also
end up on the chaff side, because of the weight factor. Chaff and empty seed can
be blown or wiped out of the bowl. I have a theory: you must be East European
to master the bowl—it has to do with hip movement while tossing—but that is
another story.

There are other implements. Face masks are essential when handling irritant
seeds (e.g., in the family Malvaceae), gloves are a must for fresh hellebore seed,
and rubber gloves with a ribbed palm are perfect for de-fluffing seed or removing
tails from Pulsatilla, Clematis or fluffy daisies. There are rolling pins and large
trays for breaking the hard Penstemon seed receptacles. Tarps are placed on the
floor with piles of unhusked legumes on top; then I dance on Baptisia or Cassia
pods while wearing heavy work boots to break the shells and release the seed.
There is even a blender for cleaning some seed that will not be damaged by this
process. Last, and of particular interest to rock gardeners, is a series of seed-
cleaning troughs which were purposely made low and wide. The rough texture
of the hypertufa is used to rub debris off seed. One learns from trial and error
which seed has a hard enough seed coat to tolerate being rubbed in the trough.

Fern spores that have been dried in large paper bags are cleaned by lightly
hitting the dried fronds against the inside of the collecting bag. The end of the
bag is kept open just far enough for hand insertion, and even then your entire
body will be covered with spore. What remains in the bag is then sifted through
the smallest mesh sieve (usually sold for powdered sugar), which removes the
bulk of the chaff that falls from the spore sac. After having cleaned a few batches
of spore, one begins to be able to identify what is the spore and what is chaff. The
spore is the smooth, dust-like material, while the chaff from the spore sac tends
to be larger and distinctly textured. This can be seen with the naked eye.

And then there are the berries. When the fruity seed starts piling up, awaiting
cleaning, the red, blue, black, white, and orange fruits are a feast for the eye and
my seed office begins smelling of strange wine. The fruited seed piles up more
often because of the extra effort required to clean it, three stages being the norm.

Seed in fruit is always collected in Ziploc bags. I keep the seed in the original
collection bags to soften. I then squish the fruits in the closed bag, using the
pressure of my hand, until a juicy mess results. This extracts the seed from the
fruit. Then I put the contents of the bag in a sieve and wash them under running water. I normally add dishwashing detergent at the final stage to help remove germination inhibitors. It is rarely possible to have the seed clean at this stage. The seed and the pulp that remain after the washing are then spread out in trays to dry; the final cleaning is done by rubbing the dry pulp off the seed with ribbed gloves or in the seed-cleaning trough. Last is either a cleaning with the sieve or tossing in the bowl.

Some seed does not respond to this technique because it has a glutinous, almost glue-like undercoat that cannot be removed by washing. Examples are Opuntia (moist-fruited species) and Chamaepericlymenum canadensis (bunchberry). The seed of these species is hard enough that one can risk putting it in a blender to clean. To avoid damaging the seed, this is done on the low setting, in small batches with the addition of water. Other very hard-coated (primarily woody) species can also be cleaned in the blender without harm. Hard-fruited species such as Malus (crab-apple) are soaked in buckets to soften the pomes before cleaning can begin.

For some berries (such as Asarum), there is no escape from tedious and labor-intensive pushing the seed out, pod by pod. When these seeds are allowed to sit on trays, exposed to air, they will either turn mushy or hard as a rock, making the final seed cleaning even tougher.

Other berries, such as Gaultheria or Vaccinium macrocarpon—which have tiny seeds encased in a mealy berry—or Epigaea repens, with equally tiny seeds formed on the outside of a juicy berry, can be dried on trays or in brown paper bags, then broken up and rubbed. Arisaema, which I used to squeeze out of their fruit, seed by seed, can be left to dry and the seed coat will rub off easily.

Finally, there is seed that needs to be dealt with soon after collection and not simply left to be cleaned later. This is the “ephemeral” or short-lived seed. These seeds must be either sown immediately or stored in a manner that will preserve their viability.

Seed Storage

Once you have collected good seed, its proper storage is crucial to its viability. Knowing how to store optimally requires knowledge of the germination patterns and longevity of individual species. While there are many variables, the most common categories for my business are:

1. Dry stored in a cool, dry place. This is the majority of seed. Shelf life can vary from a few months to some years, with the average being 1 to 2 years. All seeds that tolerate dry storage are ideal candidates for storage in the freezer, both short- and long-term. Seed must be completely dry, ideally packed in paper and placed in freezer containers with tight-fitting lids.

2. Dry stored and immediately frozen. These are seeds that tolerate dry storage but have a short lifespan. I routinely freeze immediately after harvest the seed of Pulsatilla, Anemone (woolly seeded types), Clematis, Primula, Allium, Glaucidium, Angelica, Tiarella, and others to maintain maximum viability.
Start your seed project with materials and tools handy, writes Carlo Balistrieri (p. 235). (C. Balistrieri)

Distribute seeds evenly in the pot by tapping them from a folded piece of stiff paper.
Seeds can be sown multiply in small rigid pots or individually in cell packs (p. 239). (C. Balistrieri)
Castilleja integra coupled with Penstemon strictus in a garden (p. 281). (photo, D. Nelson)

Castilleja applegatei in a rock garden feature replicating a montane meadow (p. 281). (photo, D. Joyner)
Castilleja nana with Penstemon procerus in a trough. (photos, D. Joyner)

Castilleja pilosa var. steenensis coupled with Phlox pulvinata in a trough.
Ants distribute the seeds of one group of *Erythronium* species, here *E. dens-canis* (p. 267). (A. Guppy)

Eurasian and eastern North American species have ant-attracting seeds. Left, *Erythronium japonicum*; right, *E. sibiricum*.
Western American species have seeds that are not ant-distributed and remain viable during dry periods (p. 269). Above, a form of *Erythronium californicum* with red "nectar guides"; below left, *E. revolutum*; below right, *E. tuolumnense*. (A. Guppy)
Fritillaria alburyana, a snowmelt plant of eastern Turkey (p. 285). (D. Bartlett)

Left, Fritillaria michailovskii; right, F. latifolia (p. 284).
*Fritillaria minima* in eastern Turkey (p. 286). (photos, D. Bartlett)

Below left, *Fritillaria pinardii*; below right, comparison of *F. caucasica* (left) and *F. assyriaca* (right) (p. 285).
Conandron ramondiioides (above) and Shortia soldanelloides grown from tiny, slowly developing seedlings (p. 263). (photos, Tony Reznicek)
Growing fritillaries from seed offers the chance of good color forms:
left, a population of yellow *Fritillaria pinardii* (p. 285); right, deep pink *F. stenanthera*. (J. McGary)

Garden seed can produce hybrids—left, *Fritillaria aurea* × *pinardii*, and right, *F. purdyi* × *biflora*—
that are more vigorous than one or both parents. (J. McGary)
Alstroemeria umbellata from seed collected by the grower in Chile; the seed benefits from dry storage at room temperature (p. 291). (J. McGary)

This rich color form of Cyclamen pseudibericum comes true from seed; cyclamen seed is best sown as soon as possible after ripening (p. 292).
Omphalogramma forrestii, a rare Chinese plant, created a dilemma for seed collectors (p. 295). (D. Rankin)

Ramonda myconi can be grown from seed by techniques described in this issue (p. 263). (photo, John Zabkar)
3. Cleaned and moist-packed, kept either warm or cold, depending on the germination pattern of the seed. These can be moist-packed and kept in a state of “suspension” until they receive the treatment they require to germinate. The bags are regularly opened and shaken to check moisture levels, and to ensure that air is adequate inside the plastic. In this category are Anemone (nonwoolly seeded types), Anemonopsis, Erythronium, Dicentra, Corydalis, Aconitum (ephemeral species only), Fritillaria meleagris, Astrantia, Cardiocrinum, Cornus alternifolia, Dirca palustris, Daphne, Hacquetia, Hydrophyllum, Leucojum, Panax, Ranunculus (many species), Streptopus, Stylophorum diphyllum, Trollius laxus, Triosteum pinnatifidum, Viola.

4. Dealt with as a fresh-harvest seed and sent to customers immediately after collection and cleaning, moist-packed: Trillium, Uvularia, Corydalis (some species), Helleborus, Saruma, Asarum, Sanguinaria, Claytonia, Hepatica.

5. Bulbils kept in dryish sand in the fridge: Begonia grandis, Arisarum proboscideum, and others.

Ephemeral Seed

Willows are perhaps the most notoriously short-lived seeds, as they can be dead within days if not kept moist after collection. The year I collected dwarf Salix species in the Yukon I simply placed the seed inside plastic baggies mixed with moist sphagnum I found where they were growing. These bags were on the road with me for almost two months and were perfectly viable and germinated immediately when I returned home.

Gardens North was the first seed business to use innovative methods such as sending out ephemeral seed fresh on the day of harvest, and moist-packing short-lived species to preserve viability. This has significantly increased the availability of species heretofore impossible to obtain commercially. We moist-pack most seed requiring it in vermiculite. This is done for a number of practical reasons: (1) shipping to parts of the world where soil-based substances are not allowed—even soilless mixes look too much like soil to take a chance, but vermiculite is not questioned, even in Australia; (2) the light color of the vermiculite makes it easy to see the (usually darker) seed for ease of packaging; and (3) I find it easy to maintain a proper moisture level inside the Ziploc bags with vermiculite than with other media.

The moist-packing of seed continues to fascinate me as an ongoing research project, particularly how the element of time affects the seed “suspended” at non-germinating temperatures. What I have learned thus far is that some species that require cold as a normal treatment will germinate eventually at warm temperatures if kept moist-packed long enough. I am currently testing how long seed can be kept moist-packed and what happens when it is given optimal germination conditions after various periods of time of one year or longer.
Kristl Walek is the owner of Gardens North, a Canadian seed house devoted to cold-hardy, out-of-the-ordinary perennial and woody species. She describes herself as single-mindedly absorbed by seed and germination. Her seed catalogue serves her two-pronged desire to both educate and sell. She is currently working on a book about the propagation of eastern Canadian native plants from seed. Seeds can be ordered through her website, www.gardensnorth.com.

Corrections and Addenda to Spring 2007 Issue

In the spring 2007 issue (65.2), page 151, the subject was misidentified by the editor, who mismatched a numbered image with the key provided by photographer Tanya Harvey. The plant captioned “Erigeron aureus” is in fact *Tonestus pygmaeus* (or possibly *T. iyallii*), growing at Boreas Pass, Colorado. Our apologies to Tanya, along with our thanks for the correction and her constant supply of beautiful images for this publication.

Tanya Harvey is also the photographer of the unattributed photo on p. 129 in the spring 2007 issue. Further attributions for photos taken from the Conference presentations are welcome.

Joyce Fingerut writes that the person in the photo on p. 152 of the spring 2007 issue is probably not Bill King, as stated in the caption, but probably is Dick Hildreth. Our apologies to both.

Bertil Larsson writes: “On page 25, vol. 65 no, 1 (winter 2007), the unidentified plant shown below left is, I think, *Dryadanthex tetrandra*. I saw this plant in Kirgizia 1995, and Henrik Zetterlund of the Gothenburg Botanic Garden gave me that name. It was rather common on higher, windblown places, forming tight mats on the ground and on boulders.”

If you notice a common thread in this list of corrections, there is one: the difficulty of dealing with digital photos that arrive without “transparent” file names. It’s not possible to send out the photo section for approval by all contributors in the proof stage, unlike the text, which is seen in its final version by authors. We realize that it’s time-consuming to rename files, but we will be providing some guidelines to future contributors.
Plants have a wide range of strategies for seed dispersal and establishment, and some species and groups of plants have specialized through having wind-dispersed seeds that are extremely tiny and dustlike. This includes some plants cherished by rock gardeners—many members of the Ericaceae (the heath family) and the hardy gesneriads (Ramonda, Haberlea, Conandron, Jankaea, plus others in climates warmer than my home state of Michigan) are well-known examples. (Photos, pp. 257, 260.)

These seeds present some special problems for growers. They generally germinate in rather peculiar and specialized sites in nature. For example, most Ericaceae germinate on habitats like moist, bare peat or sand, and in fine moss mats; and the hardy gesneriads, which grow on rocks and cliffs, disperse their seeds into microsites in the crevices of an outcrop. The Diapensiaceae, which includes *Shortia* and other interesting and generally difficult-to-grow plants, is another family with dustlike seeds.

Tiny seeds have little stored food, so the seedlings need to start photosynthesizing immediately. Some, in fact, require light to germinate, so they cannot be buried in the soil. Such seeds also often have no dormancy; once they alight, they can start to grow. Typically, the microsites they require for germination have not only uniform moisture but also high humidity. Growing them in open pots is not impossible, but it is difficult. Hardy gesneriads especially are also very slow-growing, so you cannot simply start them in a seed pot and put them into the garden by late summer. For me at least, maintaining suitable conditions for a long time without fail presents a particular problem. The ultimate in tiny seeds are, of course, the orchids—but they have intricate germination requirements linked with their nutrient needs (supplied in the wild by fungi) and are largely impossible to grow with ordinary methods.

Through trial and error, the best way I have found to handle many seeds like these is to germinate them in containers where you can keep them sealed. Ideal for me have been 16-ounce (about 480 cc) white plastic delicatessen containers with clear lids. I put about 4 to 5 cm (1.5–2 inches) of soil in the bottom, and a tiny pin hole in the lid. The medium will stay moist for weeks without adding...
water, so the container offers a very stable environment and near-perfect protection against pests. The soil mix needs to be fairly fine because the surface has to be made flat and firm with gentle pressure after filling the container so that the seeds stay in the light.

I usually use a mixture of fine Canadian (Sphagnum) peat and medium silica sand combined about 3:1 by volume. This mixture is not sterile, but it starts out quite “clean,” so I don’t have immediate problems with algae, fungi, or coarse mosses and liverworts. I have not had good luck with sterilizing the medium. Other mixtures may do—but if you are growing Ericaceae or Diapensiaceae you must be sure that your mix is lime-free.

Water as needed with a fine mist sprayer, and use only rainwater. Since there is no drainage hole in the container, the medium would slowly accumulate salts if you used tap water or well water from most sources. You also have to be careful to keep the soil moist, but not sopping wet.

Germination will be rapid, within a week or two at the most. If the seeds have not germinated within that time, then they likely never will. I often sow fairly thickly because it takes the seedlings a long time to get big. To keep seedlings growing as fast as possible (which is not very fast!), I raise them under fluorescent lights in the basement and give them 18-hour days at a temperature of about 60°F/11°C. The plants presumably think they are in late spring, when they would normally be growing their fastest.

Once the plants develop true leaves, I have been able to “push” Ericaceae and some gesneriads (Ramonda especially) into faster growth by inserting a few granules of a slow-release fertilizer into the medium a small distance from the seedlings. However, this has proved detrimental to some seedlings, notably Conandron, Jankaea, and Diapensiaceae.

If the seedlings are fairly dense, transplant them when they are about 3 to 4 mm across and have 2 to 4 true leaves. I sometimes do this when the plants are even smaller, but with more losses because it is so easy to damage tiny plants. I use a little stick about the size of a small toothpick to pry them out, as they have very little in the way of roots at the first transplant stage. Plant them into another container of the same type and grow them until they are between the size of a dime and a quarter before hardening them off and planting them in the open garden. For most gesneriads, it takes about a year and a half to get a seedling large enough to plant outside safely. Ericaceous plants are faster and are easier to “push” with fertilizer.

Though I have not experimented widely, this method should work for many other small seeds with similar characteristics (i.e., requirements for light and high humidity, plus slow growth). It also can be adapted for at least some fern spores.

Tony Reznicek is a plant systematist with the University of Michigan Herbarium, with research interests in the Great Lakes regional flora and sedges worldwide. He gardens on a city lot in Ann Arbor, growing both rock garden and other perennial plants, with an increasing emphasis on shade-tolerant species.
Ants and a New Look at Erythronium

Art Guppy

ABSTRACT: The genus Erythronium divides naturally into two subgenera, one that is myrmecochorous and one that is not. The two subgenera are geographically widely separated and behave very differently both in nature and in the garden.

The association in the title of Erythronium with ants may seem strange, but there is a connection that those who grow Erythronium need to be aware of, especially if they raise the plants from seed.

I discovered the association by chance many years ago when I obtained Erythronium japonicum seeds from a seed exchange and noticed little projections on the seeds. Until then my experience with seeds of the genus had been limited to species from western North America, and I was sure that none of those had such projections. Fortunately, I had been reading E. I. Applegate's 1935 monograph on the Erythronium species of western North America, as well as an article on myrmecochory, the dispersal of plant seeds by ants. Applegate had written that the Erythronium species of Europe, Asia, and eastern North America comprise an entirely different group from those of western North America. (Those two groups within the worldwide genus Erythronium mentioned by Applegate should not be confused with his well-known division of the Erythronium species of western North America into two sections, the Pardalinae and the Concolorae, on the basis or whether or not the leaves are mottled.) The fortunate juxtaposition in my mind of Applegate's grouping of Erythronium with seed dispersal by ants made me wonder if the projections on the seeds of a species from Asia could be elaiosomes.

Myrmecochory

Elaiosomes are little, fleshy projections on plant seeds that are irresistibly attractive to ants. When ants discover such seeds, they seize them and carry them away to their nests, where presumably the elaiosomes are fed to the ant larvae. The seeds are then discarded, much as we discard cherry pits, though many ant species carefully
remove the discarded seeds from the nest and drop them some distance away. With a little luck, some of the seeds are dropped where they can grow into new plants, well away from where they would compete with the parent plants. “Myrmecochory” is the name given to this extraordinary natural process by which plants make use of the remarkable energy of ants to get their seeds dispersed to new growing sites. It is such an effective way of dispersing seeds that it is known to occur in more than three thousand plant species and has been observed on every continent except Antarctica. Some well-known genera with myrmecochorous species are *Claytonia*, *Corydalis*, *Dicentra*, *Euphorbia*, *Fremontodendron*, *Trillium*, *Vancouveria*, and *Viola*.

Almost certainly this use of ant energy evolved separately in many different plant families, and consequently the elaiosomes of different families, and even different genera within a family or different species within a genus, may contain some different attractive substances, though these are generally lipids. It is evident that in some cases, in addition to providing food for the ants, or possibly instead of providing food, the elaiosomes contain substances that work directly on an ant’s instinctive urge to carry an object to its nest. For example, oleic acid, which is present in the elaiosomes of at least some *Trillium* species, is believed to trigger the corpse-carrying instinct in ants (Lanza et al. 1992).

Though there is great variation between genera and even species, generally elaiosomes emit a volatile attractive scent that is quickly dissipated after the seeds are exposed to air by the dehiscence of the seed capsules. This rather quick loss of attractive power might seem disadvantageous, but there is a way it can improve the chances for successful dispersal of the seeds. One of the purposes of myrmecochory is to avoid the accumulation of large numbers of seeds under the parent plant, where the numerous seeds would attract birds or other seed predators. However, the accumulation of discarded seeds in a midden near an ants’ nest would be even more likely to attract predators. I have frequently watched an ant pick up a seed and set off with it toward its nest, only to lose interest in its burden, drop it, and walk away. It seems evident that the scent from the elaiosome had given out and left the ant with no motivation to continue carrying the seed. Other observers also have seen ants carrying seeds for only a short distance before abandoning them. There is an obvious advantage for the seeds in this behavior, for they avoid accumulating either under the parent plant or in the ants’ midden.

Not all ants are helpful dispersers of seeds. There is a report from Australia of an ant genus that frequently consumes elaiosomes in situ, leaving the seeds under the parent plant (Anderson & Morrison 1998). In warm, fairly dry regions there are harvester ants that live by collecting seeds to use as food. There are many species, which tend to be large, fast-moving ants that range over large areas. Their activities tend to defeat the purpose of myrmecochory, as they consume both elaiosomes and seeds, though the elaiosomes nevertheless offer some protection for the seeds because other ant species may remove the seeds before the harvesters find them.

Other creatures besides ants can be attracted to elaiosomes as a source of food. In western North America a number of observers have reported seeing the
common yellow jacket wasp (Vespula vulgaris) collecting seeds from Trillium ovari-um and Vancouveria hexandra and carrying the seeds to their nests. Apparently the wasps, like most ants, consume only the elaiosomes and discard the seeds, which makes them even better dispersers of seeds than ants because they travel greater distances. Seed dispersal by wasps has come to be known as “vespico-
chory.” One commercial grower told me that wasps are a serious pest for him because they remove Trillium seeds before he can get to them.

Myrmecochory in Erythronium

At the time that little projections on the seeds of Erythronium japonicum made me wonder if some Erythronium species were myrmecochorous, the idea was nothing but a wild guess. There was absolutely nothing in the literature to suggest there was any connection between ants and Erythronium. Applegate’s suggestion of two distinct groups of Erythronium was evidently largely intuitive. To explore my idea, I needed to see fresh seeds of Erythronium of the group that Applegate had considered distinct from the western species. In my garden I had only species from western North America except for one clone of E. americanum, which flowered beautifully but failed to set seed. However, a garden shop had bulbs of E. japonicum, and a friend gave me a clone of E. americanum with which I could pollinate mine. Now I should be able to get seeds of the group that might be myrmecochorous. Already I was beginning to dream of the possibility that Applegate’s two groups might really be subgenera. Everything went according to plan and within a little over two years I had ripening capsules of both species.

It was an exciting morning when I found an E. japonicum (photo, p. 253) capsule just beginning to dehisce. I snatched it up, took a quick look at the seeds—which clearly had big, fat elaiosomes—and rushed to get my camera. Within minutes I was at a spot where I knew ants would be scurrying about in the warm morning sun. The very first seed I dropped near an ant confirmed my hopes, for the insect promptly seized it and set off toward its nest. For the next hour or so I matched wits with the ants as I tried to photograph them and they tried to escape with the seeds, but then they began to lose interest. The elaiosomes were losing their attractive power, and soon the ants paid no more attention to them than they would to pebbles.

At that point I remembered my E. americanum with its ripening seed capsules. It did not take me long to reach the plant, and I immediately saw that it was indeed my lucky day. A capsule was just beginning to open, and already several tiny ants had found it and were trying to widen the opening to get at the seeds. I quickly took up the capsule, shook off the tiny ants as being too difficult to photograph on that busy day, and headed back to my chosen ant arena. The ants gave those seeds the same reception they had given those of E. japonicum. Again I spent an hour or so taking photographs, and then again the seeds lost their attractive power. (Photo, p. 253.)

I now felt reasonably sure I knew the major characteristic that separated the two groups identified by Applegate, but I was aware that a total of 10 species
were known from Europe, Asia, and eastern North America, and I would need to ascertain that they were all myrmecochorous. That would not be easy to do, as I would need fresh seeds, and they can only be obtained by taking them from freshly dehisced capsules. I live on the west coast of North America, so I would need to obtain and grow plants from distant parts of the world, and I would need to persuade the plants to flower and set seeds. It took many years, for in most cases I could obtain the plants only by raising them from seeds, which were often difficult to get, but eventually I had all the species except *E. rostratum* and *E. propullans*, both native to eastern North America. As each species set seeds, I tested them as I had done with the seeds of the first two species, and with all of them I had equal success. It was May 2006 before the last of my species from faraway places, *E. sibiricum*, yielded its fresh seeds.

The two for which I could not obtain fresh seeds were not a serious problem. Parks and Hardin (1963), who did a thorough study of the yellow-flowered *Erythronium* species of eastern North America, concluded that *E. americanum* originated as a tetraploid hybrid of *E. umbilicatum* and *E. rostratum*, which tells us that *E. rostratum* must be closely related to the other two species and almost certainly would have elaiosomes on seeds that would be attractive to ants. *E. propullans* could be a problem because it normally reproduces vegetatively, rarely produces seeds, and apparently does so only when pollinated from *E. albidum*. Furthermore, it is an endangered species, so I could not obtain any seeds that it might produce. However, a thorough study by Pleasants and Wendel (1989) concluded that *E. propullans* derived from *E. albidum* not more than nine thousand years ago, so again I could be sure that the untested species must be closely related to a species that I had tested.

We cannot be absolutely sure that plants closely related to myrmecochorous species are also myrmecochorous, but my ultimate objective in studying these plants was not merely to determine what species are myrmecochorous. I had become convinced that the two groups identified by Applegate correspond to two subgenera, and that one of those subgenera is distinguished from the other by being myrmecochorous. A close relationship would certainly mean that species belong together in the same subgenus.

The Genus *Erythronium* Divides Naturally into Two Subgenera

I am not the only person who has thought of dividing the genus *Erythronium* into two subgenera. Shevock et al. (1990) described the two major groups as "perhaps corresponding to subgenera." However, to my knowledge, no published author has looked at the genus closely enough to describe the characteristics that identify the potential subgenera. It was my good luck years ago that I spotted the projections on the *E. japonicum* seeds and that caused me to discover that the basic difference between the subgenera is that one is myrmecochorous and the other is not.
The *Erythronium* species of western North America (photos, p. 254) have their own, distinct method of dispersing their seeds. Their firm-walled, cup-shaped seed capsules are held erect on tall, wiry stems, and when they are shaken by wind or a passing animal, the seeds are hurled out as from a catapult. Not only the capsules but also the seeds of western species are adapted to the catapult method of seed dispersal. The seeds often must remain in the capsules for weeks or even months, waiting for the powerful shake that will hurl them forth. That means the seeds must be very durable, or else they would be killed by exposure to the weather. I once kept *E. hendersonii* seeds in a packet in my refrigerator for three years and got excellent germination from them when they were sown.

As one would expect, the capsules and seeds of myrmecochorous species are adapted to their method of seed dispersal. The capsules have leathery walls that, after dehiscence (opening), curl away from the seeds, making them available to ants, and generally the mature capsules are either nodding or prostrate on the ground. There may be an exception to the general rule for the myrmecochorous subgenus. I have not had the opportunity to study *E. rostratum*, but according to published information, its capsules are held erect at maturity. That raised a question in my mind as to why a species with ant-dispersed seeds would have an erect capsule, which would seem to be out of easy reach of ants. By a stroke of good fortune, this spring I have been able to correspond with Louise Smith of Birmingham, Alabama, in the heart of the range of *E. rostratum*, and she has explained to me something which is not clear in the botanical literature. While it is true that the capsule is held erect, that position is achieved after the flower fades, by the stem bending down until it is almost horizontal and then bending up sharply near the tip. That places the capsule not far above the ground, easily reached by ants walking along the nearly horizontal stem. It seems probable that the erect position of the capsule evolved as a way of holding the seeds just out of reach of ground beetles and other seed predators, which would be common in a warm climate, while still having them accessible to ants.

There are other characteristics that distinguish the two proposed subgenera. The species of Europe, Asia, and eastern North America all produce only one flower per bulb, while many of those from western North America have several. Also, the leaf marking patterns are different. All the species of the first group usually have colorfully variegated leaves, though in both *E. sibiricum* and *E. mesochoreum* some individual plants and perhaps some populations have unmarked leaves. The marking in this group is formed of apparently random spots and blotches. In the western group there are species with mottled leaves, and species with completely unmottled leaves, and two species with only a slight trace of mottling, probably because they originated as hybrids between a mottled and an unmottled species. (*E. quinaultense* and *E. elegans* are tetraploid species that apparently originated from the crossing of *E. montanum* and *E. revolutum*.) The mottling in the western group has a somewhat symmetrical appearance, as it follows the veins in the leaf.

Having described the distinguishing characteristics of each of the two subgenera, it would seem sensible, for the sake of convenience, to name them. The
Myrmecochorous Subgenus, as I will call it here, includes *E. dens-canis*, which was the first recognized *Erythronium* species, so if I could give it a scientific name, it automatically would be subgenus *Erythronium*. It is almost as obvious that the subgenus of western North America—the group that disperses its seeds by catapult action—should be named in honor of Elmer Ivan Applegate, who wrote a monumental monograph on the western species, published in 1935 and still of great value. However, giving the subgenus a scientific name without providing a Latin diagnosis, and without having it published in a professional botanical journal or a book, which I am unable to do, would not fulfill the requirements of the International Code of Botanical Nomenclature, so I will be content with calling the western group “Applegate’s Subgenus.”

Each of the Two Subgenera Has Its Own Distinctive Diagnostic Features

Summarized from the above, the diagnostic characteristics of the Myrmecochorous Subgenus are as follows:

1. All species are native to Europe, Asia, or eastern North America.
2. The seeds have elaiosomes that adapt them for dispersal by ants.
3. The mature seed capsules generally either lie on the ground or are held in a nodding position to release the seeds. (*E. rostratum* is reported to be an exception.)
4. The mature seed capsules have leathery walls that rapidly curl away from the ripe seeds to make them available to ants.
5. The plants have no more than one flower per bulb.
6. Leaf mottling is generally present (except in some plants of *E. sibiricum* and *E. mesochoreum*).
7. The leaf mottling is in the form of apparently random spots and blotches.

The diagnostic characteristics of Applegate’s Subgenus are as follows:

1. All species are native to western North America.
2. The seeds lack elaiosomes and are adapted for exposure to the weather for weeks in an open seed capsule.
3. The mature seed capsules are held erect on strong, wiry stems and they have fairly firm walls that hold the seeds as in a cup.
4. The ripe seeds are dispersed by being flung from the capsule when the stem is swayed by wind or a passing animal.
5. All species are capable of producing more than one flower per bulb.
6. Fewer than half the species (8) have strongly mottled leaves, and 2 species have merely a trace of mottling; all other species (9) have plain green leaves. (I recognize *E. howellii* and *E. idahoense* as species, though they are not recognized in the *Flora of North America North of Mexico*.)
7. The leaf mottling, when present, follows the veins of the leaf, and thus has a somewhat symmetrical appearance.
In the Myrmecochorous Subgenus the Species Often Have Quite Different Elaiosomes

In the photos of the seeds of *E. dens-canis* and *E. japonicum* one notices a striking difference in the shape of the elaiosomes of the two species. *E. dens-canis* seeds have slender, curly elaiosomes that sometimes have the shape of a perfect corkscrew, while those of *E. japonicum* have a lumpy, round appearance that reminded me when I first saw them, right after returning from shopping, of a grocery bag stuffed with groceries. Those very different shapes are much on my mind. I wonder if the difference is confirmation of the belief that the two are distinct species, rather than being two varieties of the same species, as botanists believed in the past, and as some may still believe. That is, I wonder if elaiosomes have a taxonomic significance in addition to helping to distinguish between the subgenera. *E. caucasicum* and *E. sibiricum* both have curled elaiosomes, but they are much shorter than those of *E. dens-canis*, which may indicate that the two from western and central Asia are closely related, and have a more distant relationship to the European species. It would seem that none of the three is closely related to *E. japonicum*, with its “grocery-bag” elaiosomes.

I only recently stumbled upon the idea of elaiosomes helping to distinguish between species, so the idea is mere speculation until I have looked at the seeds of more plants of the above four species, and have had a careful look at the seeds of the species of eastern North America, which I could not do this year (2006) as various misfortunes prevented those species that are in my garden from producing ripe seeds. However, it is my impression that the elaiosomes of the eastern North American species are very different from those of the Eurasian species.

The Seeds of the Two Subgenera Have Different Needs

The seeds of Applegate’s Subgenus are durable and relatively easy to handle, though the ones from subalpine situations are a little more difficult. With low-elevation species I prefer to sow the seeds in the fall in an outdoor seedbed with shade from deciduous shrubs and no drips from overhead trees. A covering of very coarse sand provides protection from winter rains. If the seeds are not planted too closely, the seedlings can be left in the seedbed until they flower. High-elevation species may need a longer period of cool temperature than they would get outdoors. They need to go into the refrigerator in the fall. One can use the well-known moist paper towel method (see p. XX), though I prefer to use a 500-gram yoghurt or similar container, with about 2 cm of thoroughly moist sand in the bottom. Everything should be clean, and the sand should be sterilized. I sow the seeds on the sand and sprinkle on enough dry sand to not quite cover them. (The dry sand instantly takes up moisture from the moist sand.) A cover of very thin plastic film will keep moisture in but allow some passage of air. The container goes into the refrigerator until the seeds germinate. (On the bot-
tom shelf of my fridge, the temperature is about 4°C/37°F.) Then I pot the germinated seeds in suitable soil, enclose the pot in a clear plastic bag that can be opened enough to provide necessary ventilation, and place the pot in a cool place with plenty of light but no direct sunlight. Seeds that arrive from an exchange in midwinter are a problem. As seeds of the western subgenus are durable, I store them in the refrigerator until the following fall. That may be better than having them germinate after warm weather has arrived, as Erythronium seedlings do not like warm conditions.

With the seeds of myrmecochorous Erythronium, a very different procedure is likely to prove most successful. One must keep in mind the way ants "plant" the seeds and the time o the year they "plant" them. The ants leave the seeds on soil that is usually slightly moist in midsummer. That means the seeds get a fairly long period of warmth while moist before they receive the period of winter coldness that completes the germination process. You can mimic that treatment. I use sand in a yoghurt container as I have described above, but instead of putting the container in the refrigerator, I place it in a moderately warm room. About 22°C/72°F during the day and cooler at night seems about right. About two months at this temperature seems necessary, but I have not done enough experimenting to be sure what period is ideal. After the seeds have had their warm period, they go into the refrigerator and are treated the same as seeds of the other subgenus. The above procedure worked very well for seeds of E. sibiricum that arrived in late October, were given two months of moist warmth, and went into the refrigerator about January 1. Almost all of those seeds germinated in February and early March. I have not used this method for very long and seeds of the Myrmecochorous Subgenus are difficult to obtain, so I still have much to learn about them. With fresh seeds of this subgenus from my own garden, I have given them a week to dry in a cool place after I collected them, and then I sowed them in an outdoor seedbed where they could have their necessary period of moist warmth. That worked well.

While I discovered by watching ants how the dormancy of seeds of this subgenus is broken, others have learned the same thing simply by observing the seeds. A 1985 paper by J. M. Baskin and C. C. Baskin gives valuable information on the germination of E. albidum seeds. Their study showed that E. albidum seeds are underdeveloped at the time they are dispersed in late May and remain dormant under leaf litter during the summer months. The embryos in the seeds gradually grow from early September through late January, with the most growth occurring in October and November, and with germination occurring in late winter and early spring. Although they found that the embryos require low temperatures for growth, they also found that absolutely no growth takes place unless the seeds have first had the period of moist warmth during the summer months. In brief, warm stratification followed by cold stratification is required to break the dormancy of E. albidum seeds. That is exactly what I found with other species in the Myrmecochorous Subgenus.

Seeds of the Myrmecochorous Subgenus that arrive in midwinter can be an even worse problem than those of Applegate's Subgenus because they may not be durable enough to survive until the following fall. In 2006 a correspondent in
Oregon reported that seeds of *E. sibiricum* and *E. japonicum* that she received in January were planted in pots that were placed outdoors, and they germinated well in late spring. Perhaps those seeds were successful without any warm period, but it seems likely that either the February weather in Oregon was mild enough to give them something rather like a warm period, or perhaps more likely, the seeds were obtained from a well-informed dealer who had given them their necessary period of warm stratification.

*Erythronium* seeds are unpredictable things because not only the different subgenera but also different species and even different local ecotypes have evolved different needs. One can only use one’s knowledge of the plants to try to improvise a treatment that will suit them. As all *Erythronium* seedlings like cool conditions, in 2006 I tried to improvise a way to give late-germinating seedlings protection from the warmth of late spring and early summer. I planted the late arrivals in an outdoor seed bed with considerable shade. Over them I placed a frame with a strong wire mesh supported about 10 cm above the soil, and on that I arranged narrow strips of wood to break the force of any sun that reached the bed. Every evening, without fail, I sprayed the seedlings lightly with water. Four groups of seedlings got this treatment, and although there were some losses, most stayed green long enough to make me hope they have formed strong bulbs. Included in this experiment were a half-dozen germinated seeds of *E. quinaultense* I had collected while photographing the species in mid-May in its montane habitat north of Lake Quinault in Washington state. I arrived home with those little green shoots, each with a seed at its tip, at the beginning of a spell of very warm weather, but they survived nicely. By early April, 2007, I was pleased to see that my improvised treatment of late-germinating seedlings, including the ones from near Lake Quinault, was a success, as in each compartment of the seed bed little second-year seedlings were shooting up. Growing erythroniums from seed involves being very good at improving.

**References Cited**


Art Guppy of Duncan, British Columbia, is a noted grower of rhododendrons and other ericaceous plants as well as of *Erythronium* species.

*Erythronium grandiflorum*, drawing by Phyllis Gustafson.
Storage of Seeds

Norman C. Deno

It was a natural extension of my studies on seed germination to look at seed storage. I studied storage lives of 163 species over 5 to 15 years, using dry storage at 70° F/21° C (room temperature), 40° F/4.5° C (refrigerator), and 0° F/-18° C (freezer). [Henceforth all temperatures are stated with Fahrenheit first and Celsius second.] For 32 of these species, I also studied storage under moist conditions. I personally collected all 163 species so that their exact storage history was known.

I studied an additional 760 species using only dry storage at 70°/21°. Many of these were commercial samples. Although their exact storage history was uncertain, this was not so critical for studying dry storage at 70°/21° because any previous storage was probably at that temperature. I envisioned publishing a book titled Seed Storage Theory and Practice, but because the market for it would be so limited, I now present a condensed summary of my results.

Results and Implications

1. Storage lives are far longer when seeds are stored in a refrigerator around 40°/4.5° than a room temperatures. This has been recognized for years in the horticultural literature.

2. Although death rates are slower when seeds are dry-stored in a freezer around 0°/-18°, this type of storage can be fatal because of the formation of ice crystals. The consequent expansion ruptures cell walls. Examples of species whose seeds died faster at 0°/-18° than at 40°/4.5° are Arisaema dracontium, A. triphyllum, Berberis thunbergii, Eranthis hyemalis, Gingko biloba, Hesperis matronalis, Hibiscus syriacus, Koelreuteria paniculata, Lilium centifolium xhenryi, Maclura pomifera, Pyrus calleryana, and Viburnum dentatum. Supercooling is erratic, so that data on storage at 0°/-18° will lack reproducibility, particularly because of the viscous nature of the aqueous phase in seeds. Crystallization may be delayed for years in such viscous solutions: recall how honey may remain clear for years before fructose crystallization starts.

3. The lives of seeds varied enormously from species to species. For example, seeds of Salix arctica (a dwarf willow) dry-stored at 70°/21° are dead in two
weeks, whereas some seeds from other genera stored at that temperature have been found to be 100% viable after 150 years.

4. Death rates follow a “time clock” rate curve. Viability persists for a period, and then death follows in a relatively shorter period. The question arises as to whether older seeds produce less vigorous seedlings. I definitely observed this for *Salix arctica* dry-stored at 40°/4.5° and 0°/-18°, but other species showed no marked effect.

5. There is no evidence that storing seeds in sealed containers increases storage life, despite this being a popular practice.

6. It is doubtful that artificial drying of seeds has a major effect. I conducted extensive studies on *Dendrocalamus strictus* (a clump-forming bamboo). Storing the seeds in open packets and in sealed packets, with or without desiccant, had no varying effects. However, claims appear from time to time that artificial drying of seeds increases storage life. In general, the effects of drying reported were small relative to the greatly increased storage lives at lower temperatures.

7. Experiments on storing seeds in inert atmospheres such as nitrogen, argon, and carbon dioxide, reported in the references cited, gave inconclusive results. This suggests that the dying of seeds is due to restructuring of polymer molecules and does not involve water or oxygen. This is in accord with the large effects of temperature, the lack of effects of storing seeds in sealed containers with or without desiccant, and the fact that seeds with impervious coats die in storage just as other seeds do.

8. The government laboratory at Fort Collins, Colorado, stores seeds at liquid nitrogen temperatures. Seeds have even been cooled to less than a degree above absolute zero and have retained viability. It is likely that seeds stored at such low temperatures will remain viable indefinitely because there is so little molecular motion. If the cooling and rewarming are done rapidly, there is little chance of ice formation; however, slow cooling and warming could be fatal.

9. Moist storage is not usually done, but of the 32 species in which I studied it, six species showed much longer storage lives when kept moist at both 70°/21° and 40°/4.5°. These were *Cornus stolonifera*, *Euonymus alatus*, *E. europeaeus*, *Ilex verticillata*, *Iris pseudacorus*, and *Salix arctica*. Moist storage at 0°/-18° generally gave shorter storage lives, presumably because of ice formation. Moist storage is applicable only to species that typically germinate at 40°/4.5°, or in alternating conditions of 40°-70°/4.5°-21°, 70°-40°, and other complex patterns. The data on moist storage also show that artificial drying can be injurious to some species.

10. For seeds dry-stored at 40°/4.5° or 0°/-18°, viability cannot be tested simply by placing the seeds in moist media at 70°/21°. For example, *Campanula latifolia* is a D-70 germinator, requiring a period of dry storage at 70°/21° to destroy germination inhibitors. Its seeds dry-stored at 40°/4.5° or 0°/-18° for two years gave only 35% and 10% germination, respectively, if placed directly in moist conditions at 70°/21°. However, if after removal from storage they were dry-stored for three months at 70°/21°, they gave 100% ger-
mination, showing that they were really viable but needed the conditioning of three months in warmth and dryness. The conditioning chemistry is taking place at the lower temperatures, but much more slowly.

11. Here is a major question that does not seem to have been recognized heretofore: Does fresh seed or conditioned seed have a longer storage life? For example, take a typical D-70 germinator. During the dry storage, chemical changes are taking place inside the seeds, so that the seeds at the end of this conditioning are different from fresh seeds and could have different storage lives. It might be presumed that fresh seed would store better, but in science, beware of presumptions. It is evident that samples of commercial seeds and those from seed exchanges have already been subjected to several months of dry, warm storage. If such seeds are then placed in dry storage in refrigerator or freezer, we are really studying the storage of conditioned seeds.

12. The problem stated above becomes even more complex for species with extended germination patterns. For example, *Campanula americana* has a 70-40-70L (L = exposed to light) germination pattern. Say there are three separate forms of its seed available for storage: fresh seed; seed that has been subjected to three months moist storage at 70°/21°; and seed subjected to a further three months moist at 40°/4.5°. Again, these three forms are chemically different and probably will have different death rates and different storage lives.

Groups with Similar Storage Responses

In order to give some guidance, I have organized the 163 species studied into the following four groups. Remember that these are oversimplifications. All species studied are valued in horticulture.

**Group 1** is composed of species that flower early in the year and ripen their seeds within a month after flowering. The seeds disperse and germinate immediately. Examples are species of *Populus* (poplars and cottonwoods), *Salix* (willows), and *Tussilago* (coltsfoot). These seeds have cottony tufts that aid in wind dispersal. They appear to avoid germinating before dispersal simply by the seed pod’s preventing access to water. Seeds in Group 1 have very short lifetimes when dry-stored at 70°/21°; their lives are much increased by storage at 40°/4.5°, but they are still short-lived relative to other groups. About 6% of the 163 species had this behavior.

**Group 2** is composed of certain nuts, many species of the Ranunculaceae (buttercup family), and many woodland plants. Although they show much variation in germination patterns and rates of dying, most are dead after one year of dry storage at 70°/21°. About 42% of 163 had this behavior.

**Group 3** consists of seeds with D-70 germination patterns. The common garden annuals and vegetables are almost all in this group. The fact that D-70 germinators require a dry, warm period to condition them for germination requires that they must be able to survive at least several years of dry storage. Generally, they retain viability for 5 to 15 years at 70°/21°. Storage lives do not correlate with the size of seeds. Some very small seeds, such as those of *Kunzea*, have been found to be 100%
viable after 20 years dry-stored at 70°/21°. As with all seeds, storage life is much prolonged at lower temperatures. About 40% of my sample had this behavior.

**Group 4** consists of species that retain viability on the order of 50 to 100 or more years. Two types of seeds fall into this group. Those with impervious seed coats (many Fabaceae [pea family] and Malvaceae [mallow family]) generally have long lives in storage. The second type is seeds that require light for germination. Work at Michigan State University initiated in 1879 by W. J. Beal shows that several species of *Verbascum* (mullein) retain viability for over 150 years. My own experiments are only 15 years old, but they confirm the long life of *Verbascum*. Studies by J. F. Harrington in 1906 and by M. P. Becquerel in 1934 on seeds stored at the Museum of Natural History in Paris found some species with very long storage lives. About 12% of my sample falls into this group.

The past literature is reviewed excellently in the six general books listed in the References. However, all this past literature was either anecdotal or, at best, reported studies in which variables were not controlled. Only Lela Barton’s work on *Lilium regale* (1947) is comparable to my current work in that rates of dying were measured and variables were controlled. There have been reports that wheat seeds in mummies’ hands, lotus seeds in ancient peat beds, and seeds from ancient rodent stores in the Arctic maintained some viability, but these reports are probably erroneous (Bewley and Black, 1985).

**Acknowledgments**

Many people have contributed seeds and information to my program, and this is gratefully acknowledged. In particular, Phyllis Farkas of Webster, New York, contributed a collection of seeds of 242 species that had been dry stored at 40°/4.5° for ten to fifteen years. My own work had studied 126 of these species, so there was some duplication. The second group comprised seeds of 127 species collected by a Mr. and Mrs. Sanderson and given to me by Lucy Boyce. These had been dry-stored at 70°/21° for three to ten years. Only 29 of that 127 were still viable, and 30 were already in my study. Many of the latter group were roadside weeds, but there was no marked difference in patterns from the more horticulturally valued species studied.

**References**


Techniques for Growing Castilleja in the Garden

David Nelson and David E. Joyner

The two authors met in July 2006 at the International Interim Rock Garden Conference at Snowbird, Utah. We found that both of us have experimented with Castilleja (Scrophulariaceae) propagation for at least ten years. Furthermore, both of us have had similar experiences trying to grow this hemiparasitic (facultative parasite) genus in Utah and Washington state. Dave's initial attempts at growing Castilleja in Utah involved seed from C. miniata, C. rhexifolia, and C. applegatei collected in the Wasatch and Uinta mountains. Early attempts in Washington involved C. miniata seed collected in the Cascades. However, both of us soon expanded our efforts to include commercially available Castilleja seeds, as well as seed obtained from seed exchanges. We thought it useful to our NARGS colleagues to provide a narrative of our Castilleja growing techniques (with modification of Norman Deno's stratification process), as well as a comparison of the results from two western U.S. locations.

The propagation of many Castilleja species can be achieved with reasonable ease (refer to Tables 1 and 2). Our classification of "horticultural feasibility" was in response to the following factors: (1) viability of the seed, either commercial or collected, (2) ease of seedling transplantation or survival from germination trays to permanent bed/trough, (3) longevity once established (species labeled "easy" flourished for at least 2 years, while moderately difficult made it through the first season), (4) narrow or broad growth requirements (survive in a wide variety of habitats or restricted to a narrow niche), and (5) whether the plant grows in the open garden or is restricted to a trough. However, one must understand that other factors may also be involved. Furthermore, no one method worked for all of the species tested. Nevertheless, the following information should allow you to duplicate our results with the species defined as "easy." We note that C. chromosa is used throughout our work, rather than C. applegatei subsp. martini or C. angustifolia var. dubia.

Norman Deno's (1993) stratification process has been confirmed for Castilleja by Lawrence and Kaye (2005), Luna (2005), and Nelson (2006). In general, seeds are placed on a damp paper towel inside a loosely closed plastic bag and stored in a refrigerator at 5°C/40°F for 1 to 3 months. Both of us initiate the stratification process in December or January. Unfortunately, germinated seedlings often pen-
etrate the wet paper towel with their radicles (first roots). The seedlings are then difficult to remove from the wet towel using tweezers and many may be lost. Joyner, in Utah, has developed a technique to avoid this problem. Approximately 0.25 teaspoon of damp Whitney Farms seed-starting mix, or equivalent, is placed in each bottom corner of a plastic sandwich bag. Several Castilleja seeds are added to each pocket of soil and mixed by flipping the bag. These filled corners are twisted separately to enclose the soil/seed mix and rubber bands are used to isolate the corners. This method allows for two starts of the same species or different species. Usually, 1 to 2 months of stratification is required for most Castilleja species. Sometimes the process is allowed to continue for 3 months if transplantation is inconvenient. The sandwich bags are checked periodically for seedlings (their roots can be seen at the bag interface). If the seeds have germinated, the seedlings and mix are immediately transplanted to a small pot. One must be aware that C. nana, C. pulchella, and other alpine species often germinate early (after considerably less than 3 months’ cold stratification), while the larger desert and montane paintbrushes rarely, if ever, germinate during the 3-month stratification period.

Once germinated, most Castilleja seedlings react poorly to being transferred to germination trays or pots. One solution to this problem is to deposit cold-stratified seeds into 72-well germination trays in late February or early March, and use artificial lights and house temperatures to germinate the seeds. This approach generally produces rapid germination, but the seedlings respond badly to the lack of sufficient light and the high humidity typical of enclosed germination trays. Under these conditions, one must be aware of fungal predation (damping off). These trays can be placed outside, but germination tends to be sporadic under outside conditions. Once the time requirements of stratification are defined for a species, the process becomes more efficient.

Transplanting, "coupling" (associating the hemiparasitic Castilleja with a compatible host plant such as a penstemon), and keeping Castilleja alive through the first year following germination is a major concern. If the soil becomes too dry, even desert species inevitably shrivel and die. Both of us lack the space and time to maintain seedlings in small pots throughout the first year. One solution to this problem is the use of large plastic tubs (approximately 1 m by 0.5 m with 30 cm depth) filled with a suitable soil mix. Joyner finds that up to 30 paintbrush plants can be germinated and grown, along with their hosts, in a single tub. The 30-cm (1 foot) depth enables the seedlings to survive the hot, dry Utah summer, while protecting the roots from freezing temperatures during the cold winter months. In early spring, the front of the tub can be carefully cut away and the semi-dormant paintbrushes and hosts transplanted together into suitable locations. He also has had success with this method by cutting away both ends of the tub and sliding the intact soil mass with plants into a garden hole of similar depth and dimensions; the sides and base of the tub are removed subsequently by sliding the plastic out from under the soil mass.

In Washington, Nelson places the host and paintbrush together within 2 cm when the latter develops its first true leaves. The pair is placed into a small peat pot with appropriate soil and kept on a shaded deck from March through May. This
approach requires that the pots be moved to a warm garage at night. By June, the
pairs are transplanted into suitable spots in the garden. Obviously, this requires
considerable effort and emphasizes the relative ease of Joyner’s tub procedure.

It must be emphasized that host and paintbrush must have compatible horti-
cultural requirements. Our experience proves that water, soil, and light conditions
must be compatible for both members of the host-parasite pair. An example of
incompatibility is coupling the xeric *C. integra* with *Penstemon ovatus*, a species from
the rainy side of the Cascade Mountains; another is coupling the very xeric *C. angusti-
tifolia* with a moisture-loving gentian. More suitable arrangements would link *C.
integra* with *Penstemon strictus* (photo, p. 251), and *C. angustifolia* with an *Astragalus*.

One additional technique that has been utilized by several colleagues (see the
forum “Castillejas in Cultivation,” 2003) involves placing stratified seed next to
an established host species and allowing Mother Nature to germinate the
*Castilleja* seeds. Our experience suggests this procedure frequently takes 1 to 2
months, or even several years for the seeds to germinate. Furthermore, both our
gardens are attractive to seed-eating birds (especially California quail), so the
seed must be hidden at the base of the host. This method reduces the distance
the paintbrush haustoria (the root processes that link parasite and host) must
extend to the root system of its host species. Larger species, such as *C. miniata*, *C.
chromosa*, and *C. linariifolia*, tend to establish well via this approach in Utah. How-
ever, in Washington, only 10% of *C. integra* germinated when deposited adjacent
to established *Penstemon strictus* or *P. eatonii*.

In general, we both agree that paintbrushes are probably not host-specific,
although our experience suggests that some host species are more suitable than
others. Again, such selectivity may depend upon the compatibility of cultural
requirements. Host root structures may also be important. Thus, better germi-
nation and establishment was achieved when stratified *Castilleja* seed was placed
adjacent to the fescue *Festuca idahoensis*. The rapidly spreading, fine roots of
grasses may provide a broad target for the paintbrush haustoria. Often grasses
allow paintbrushes to survive until the roots of a more desirable plant become
available. Table 3 gives a selection of compatible pairs utilized in Utah. Success-
ful pairs noted in Washington have been reported previously (Nelson 2006).

Several observations from Joyner’s Utah experience may prove useful to rock
gardeners trying to lure *Castilleja* into their gardens. For instance, *C. linariifolia*
behaves as a classic “weed” in his garden! It grows under most garden conditions,
and its seeds exhibit an excellent germination rate approaching 100%. Unfortu-
nately, this plant is not attractive. Another near-weed in his Salt Lake City garden
is *C. occidentalis*. This is a very attractive alpine species with light yellow bracts, so
its weediness is overlooked. However, his favorite “easy-to-grow” paintbrush is
*C. chromosa*. Seeds from this desert species were collected in the House Range in
western Utah (Great Basin Desert). *C. chromosa* is one of the earliest plants to
bloom (late March into April) in Joyner’s yard, along with the subalpine *C. apple-
gatei* (p. 251). However, he found that *C. chromosa* is most successful when grown
in imported “desert” soil; otherwise, it generally doesn’t survive beyond the first
season. The desert form of *C. chromosa* has purplish stems with dark blood-red
bracts. Joyner has also collected seed from a montane form of *C. chromosa* found at 2500 m in western Colorado. This latter form appears morphologically different, having green instead of purple stems and red-orange bracts.

The Texas annual *C. indivisa* survives reasonably well in Utah when coupled with a grass host, but this paintbrush has generally failed to set seed. In Washington, a few plants of *C. indivisa* have reseeded when coupled with *Penstemon strictus*. They were planted in a wet but well-drained area that seems to allow both species to bloom from July through mid-October. Nevertheless, a constantly renewed seed supply is necessary to maintain these annuals in Utah or Washington state.

The moderately difficult or difficult species tend to be desert or alpine species and thus are very demanding in their cultural requirements. *C. scabrida* and *C. thompsonii* are equally demanding xeric paintbrushes. *C. scabrida* originates in the hotter deserts of eastern Utah, while *C. thompsonii* hails from eastern Washington (the Mid-Columbia Basin). Both plants require equally xeric hosts. However, the hosts must be robust enough to provide water for both plants, since most *Castilleja* have quite high transpiration rates. Joyner has had limited success with these species because they do not readily produce viable seed.

We also include several subalpine to alpine species in our difficult-to-cultivate category. For instance, both varieties of *C. pilosa* are very temperamental regarding wet winter conditions. *C. pilosa* var. *pilosa* is a subalpine from California and really abhors wet roots in early spring, while *C. pilosa* var. *steenensis* hails from southeastern Oregon. Seed viability also seems to be a problem for both varieties. Both tend to be rather drab, but their difficulty makes them worth the challenge.

As can be noted from our experience, one probably requires a number of suitable niches in the garden if both alpine and xeric *Castilleja* are to be attempted. Both of us have independently learned about matching hosts with paintbrushes. We suggest trying one or two of the paintbrushes from the easy category if you have not tried propagating them before. Paintbrushes do require a bit of work, but the comments from your friends will be worth the adventure.

### Table 1. Horticultural feasibility of *Castilleja* conducted in Salt Lake City, Utah.

<table>
<thead>
<tr>
<th>Easy</th>
<th>Moderately Difficult</th>
<th>Difficult</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. chromosa</em></td>
<td><em>C. applegatei</em></td>
<td><em>C. angustifolia</em></td>
</tr>
<tr>
<td><em>C. hispida</em></td>
<td><em>C. arachnoidea</em></td>
<td><em>C. chrysantha</em></td>
</tr>
<tr>
<td><em>C. integra</em></td>
<td><em>C. cinerea</em></td>
<td><em>C. oresbia</em></td>
</tr>
<tr>
<td><em>C. linariifolia</em></td>
<td><em>C. indivisa</em></td>
<td><em>C. pilosa</em> var. <em>pilosa</em></td>
</tr>
<tr>
<td><em>C. occidentalis</em></td>
<td><em>C. miniata</em></td>
<td><em>C. pilosa</em> var. <em>steenensis</em></td>
</tr>
<tr>
<td><em>C. parvula</em> var. <em>parvula</em></td>
<td></td>
<td><em>C. rubida</em></td>
</tr>
<tr>
<td><em>C. suksdorfi</em></td>
<td></td>
<td><em>C. scabrida</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>C. sulphurea</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>C. thompsonii</em></td>
</tr>
</tbody>
</table>

*Annual paintbrush*
Table 2. Horticultural feasibility of *Castilleja* grown in Richland, Washington.

<table>
<thead>
<tr>
<th>Easy</th>
<th>Moderately Difficult</th>
<th>Difficult</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. <em>exserta</em></td>
<td>C. <em>chromosa</em></td>
<td>C. <em>christii</em></td>
</tr>
<tr>
<td>C. <em>haydenii</em></td>
<td>C. <em>rhexifolia</em></td>
<td>C. <em>coccinea</em></td>
</tr>
<tr>
<td>C. <em>hispida</em></td>
<td>C. <em>rupicola</em></td>
<td>C. <em>covilleana</em></td>
</tr>
<tr>
<td>C. <em>indivisa</em></td>
<td></td>
<td>C. <em>nivea</em></td>
</tr>
<tr>
<td>C. <em>integra</em></td>
<td></td>
<td>C. <em>parviflora</em></td>
</tr>
</tbody>
</table>

*Annual paintbrush

Table 3. Successful *Castilleja* hosts utilized in the Utah garden.

<table>
<thead>
<tr>
<th><em>Castilleja</em></th>
<th>Host(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. <em>angustifolia</em></td>
<td><em>Astragalus simplicifolius</em></td>
</tr>
<tr>
<td>C. <em>applegatei</em></td>
<td><em>Astragalus</em>, <em>Erigeron</em>, <em>Eriogonum</em>, Townsendia</td>
</tr>
<tr>
<td>C. <em>chromosa</em></td>
<td><em>Astragalus</em>, <em>Erigeron</em>, <em>Eriogonum</em>, Townsendia</td>
</tr>
<tr>
<td>C. <em>integra</em></td>
<td><em>Eriogonum</em> spp.</td>
</tr>
<tr>
<td>C. <em>linariifolia</em></td>
<td><em>Artemisia tridentate</em>, <em>Eriogonum</em>, <em>Penstemon</em>, and prairie grasses</td>
</tr>
<tr>
<td>C. <em>miniata</em></td>
<td>Montana meadow mix*</td>
</tr>
<tr>
<td>C. <em>nana</em></td>
<td><em>Primula rusbyi</em></td>
</tr>
<tr>
<td>C. <em>occidentalis</em></td>
<td><em>Penstemon procerus</em></td>
</tr>
<tr>
<td>C. <em>parvula</em> var. <em>parvula</em></td>
<td><em>(Arenaria</em> spp.</td>
</tr>
<tr>
<td>C. <em>pilosa</em> var. <em>pilosa</em></td>
<td><em>(Arenaria</em> spp.</td>
</tr>
<tr>
<td>C. <em>pulchella</em></td>
<td><em>Primula allionii</em></td>
</tr>
<tr>
<td>C. <em>rhexifolia</em></td>
<td>Montane meadow mix</td>
</tr>
<tr>
<td>C. <em>schizotricha</em></td>
<td><em>Linum kingii</em></td>
</tr>
<tr>
<td>C. <em>sessiliflora</em></td>
<td><em>Astragalus desparatus</em></td>
</tr>
<tr>
<td>C. <em>suksdorfii</em></td>
<td><em>Anemone multifida</em> and <em>Gentiana</em> spp.</td>
</tr>
</tbody>
</table>

*The Montana meadow mix consists mostly of Asteridae such as *Aster*, *Campanula*, *Erigeron*, *Mertensia*, but no grasses.

References


Dave Joyner grows 26 species of *Castilleja* and many other natives in his Salt Lake City garden, while Dave Nelson is attempting to replicate a subalpine setting in Richland, Washington.
Small Fritillaries in Eastern Turkey

Dick Bartlett

To the uninitiated, fritillaries (Fritillaria species) may seem dull and uninteresting, but, of course, to the expert they are not. I must say, right off, that I was one of those less enthusiastic individuals, although I had grown several species in my garden. Here in Denver, some of them can be finicky to grow in the rock garden, not always showing up or flowering every year. As a group of bulbs, they bloom early and disappear in the hot summer months. Many are insignificant in flower, often greenish, dull purple, or brown. But one needs to understand the flowering mechanism involved to appreciate them. The beauty and coloration are inside the bell, and there is the attraction for pollinators.

As a life member of the Alpine Garden Society (AGS) of Great Britain, I frequently go on their well-organized and inexpensive tours. When in 2005 they offered a trip to Turkey, I was excited, because Denver's climate is very similar to that of eastern Turkey. Also, I wished very much to see the Oncocyclus iris species found in that part of the world, and I did. However, the trip was led by a couple, Bob and Ranveig Wallis, who are fritillary experts. Hence, my fritillary education began. Because of their interest, the trip was planned for the last two weeks in May.

In total we saw ten "frits," as well as many alpines and subalpines. We saw numerous orchids, and many bulbous plants such as Corydalis, Colchicum, and especially Bellevalia, because the trip was in early spring. In addition, the eighteen of us got to see Turkish culture, the landscape, its people, and the Kurdish people. In all, it was a very successful trip. We flew to Trabzon, followed the road south over the Zigana Pass, and then went east to Erzurum. At Erzurum we had three days for side trips. From there we continued east to Dogubayazit with its view of Mt. Ararat, and then traveled south to go around Lake Van from west to east. At the town of Van we again had side trips for three days.

The first Fritillaria species we encountered was at the top of a small hill half way to Erzurum, and it was one of my favorites. Fritillaria latifolia (p. 255) is not over 3 inches (7.5 cm) tall, with a huge bell flower about 1.5 inches wide and nearly touching the ground. It is very difficult to see because of its low growth and dull purple exterior, and one has to be careful not to step on it. If you get involved with fritillaries you quickly learn to look inside the bell and see the
beauty inside. Often there is a “checkered” (or “tessellated”) pattern, usually maroon or brownish. In the commonly grown F. meleagris, you can see this tessellation on the outside. F. latifolia excels in this quality on the inside of its huge bell.

Also on the way to Erzurum was F. crassifolia subsp. kurdica. It is greenish brown and small, but the tessellation peeks out at the outer margins of tepals (the segments of a flower in the lily family, loosely called “petals” but actually both petals and sepals). It seemed to be the most widespread species in eastern Turkey.

After you go over Zigana Pass and turn east, you are traveling along a west-to-east trending, deep valley. The first valley is short, and Kop Pass connects you to the longer valley that continues all the way to Dogubayazit. Most of the fritillaries were found on the slopes of the low hills alongside these two valleys. Before you come to Erzurum, going east, you come to the end of the first valley and cross a pass to the next valley. On the western side, approaching the pass, was Fritillaria pinardii, not a particularly showy one—about 6 inches (15 cm) high, showing a touch of yellow at the bottom of the bell. In this location F. pinardii grows on fossiliferous limestone, but this is not always so.

If this frit didn’t seem too ordinary, the next one far excelled it. As we went up the grade past a monument at Kop Pass, we took a side road to a radio tower. Here we found what at the right season would be an outstanding natural rock garden with Acantholimon, Dianthus, Pedicularis, and other interesting small alpine plants, but only the yellow Draba species were in bloom at this time. Yet just above this spot was Fritillaria alburaiana (photo, p. 255), one of the very best we saw. Again, it is less than 3 inches tall, but its bell is dark pink or reddish. Fortunately, a few of them had their bells fully open and extended in glory. With back lighting, we could see the faint hint of tessellation in the pink petals.

Further along the longer valley, I noted three more fritillaries. The first two are difficult to tell apart without careful close examination: Fritillaria assyriaca and F. caucasica. Both are about 6-8 inches (15-20 cm) tall, with bells of dusty dark purple with a “gunmetal” sheen. Inside the bell are varying tints of reddish purple or yellow. For our edification, Rannveig dissected the two species and displayed them on a table so we could see how they differed (photo, p. 256). F. caucasica has purple interior petals and a smaller stigma, while F. assyriaca has a larger stigma and yellow interior and tips. I was lucky to see an unusual example of a 12-inch-tall F. caucasica, which I photographed against the sky. The third species was just off this valley, south of the town of Horasan—F. michailovskiyi (p. 255). This one can get taller in the garden but was only about 4 inches (10 cm) high at this site. [Height varies among populations and does not necessarily depend on cultural conditions. —Ed.] F. michailovskiyi has a fairly large bell with a very nice flared yellow margin. Like several other plants seen in Turkey, this one had an all-yellow variant growing next to it.

With the exception of the Pontic Mountains to the north, the landscape is treeless and the vast amount of land is used for flocks of goats and sheep. The most startling surprise comes when you realize there are no fences, and only rarely a series of very low walls. The valleys are wide and very flat, and this is not where the fritillaries grow. They seem to prefer the rounded foothills surrounding the valleys and below the high mountains. In most cases, where they grow the
soil is stony, well-drained but rich, and probably mildly alkaline. *F. crassifolia* in two places we visited grew in rich limestone scree. Mt. Ararat is an impressive sight at 16,945 feet (5165 m) above a flat valley less than a mile (1609 m) high. There are a few other volcano mountains in the area as well. Lake Van, though much less saline than the Great Salt Lake in Utah, is known as a “soda lake.”

Now we come to the last two fritillaries. On the west end of Lake Van is the town of Tatvan. Just to the north of the town is a massive caldera, Mt. Nemrut, much like Crater Lake in Oregon but much broader: 49 square miles (127 km²) of crater with 2000-foot (610-m) walls. It is this volcano that blocked off the outlet and thus created Lake Van. Toward the bottom of the crater are two species, of which *F. pinardii* has already been mentioned. The other one is *F. minuta* (p. 256), a small plant with a brownish exterior and orange interior. The inflorescence is not quite bell-shaped, but more widely spreading and pendent. Its flower is less than 0.75 inch long and the scape is under 2 inches in height, but it is not the smallest species we saw. Southeast of the town of Van, we entered the high, snow-topped mountains. Just below the snow patches we were shown *F. minima*, which turned out to be the smallest species. It is an all-yellow miniature, 1.5 inches tall, growing in very rocky soil. It also was, I believe, the one to be found at the highest elevation.

Although there were many military personnel around and occasional passport check stops, the military were extremely friendly to us, as were the Turkish people and Kurdish nomads. We also visited several ruins and other ancient sites, such as Dogubayazit’s famous Ishak Pasha Palace where it once guarded the old Silk Road; and Hosap Castle, east of Van near the Iranian border, on a hill above the town of Hakkari, also on the Silk Road.

It has been my intention to pique your interest in fritillaries a bit with this article, although I am no expert on them. As a reference to these Turkish species, I suggest *Dwarf Bulbs* by Brian Mathew (1986) [for more recent references, see below]. All the fritillaries mentioned above are listed there; however, he groups *F. caucasica*, *F. pinardii*, and *F. minuta* under *F. armena*. In closing, I have unexpectedly gained a true respect for and interest in fritillaries, and since our Denver climate is similar I intend to try and grow some of those from eastern Turkey.

Further Reading

The editor, who grows and sells a great many *Fritillaria* species, suggests the following. *(The Gardener’s Guide to Growing Fritillaries* is not recommended.)


For information on the Fritillaria Group of the Alpine Garden Society, visit www.fritillaria.org.uk

Dick Bartlett and his wife, Ann, garden in Denver. Dick is the current president of NARGS and has long been active in the Rocky Mountain Chapter.
Every summer I lift and repot about half of the 1300-plus kinds of bulbs I grow plunged in cold frames and sell the surplus bulbs through an informal list. It always surprises me how avid other gardeners are to buy certain kinds, such as species *Narcissus*, that can be grown easily from seed. I acquired around three-quarters of my collection by purchasing seeds or getting them through exchanges or wild collection, beginning around 1990. I was inspired to do this when the late Molly Grothaus, a fine bulb grower, brought a pot of *Fritillaria raddeana* in flower to a NARGS chapter meeting. She mentioned that she had grown the plants from seed, and noticing my enthusiasm, she later gave me some of the seeds they had set. Today I still have half a dozen of the original bulbs grown from those seeds.

Why, then, doesn’t everyone who wants bulbs grow them from seed? Some say, “I don’t have a place to grow seeds.” In most climatic regions in North America, all you need is a flat place that can, perhaps, be covered during inclement weather. Even the worst carpenter in the world (and that would be myself) can knock together a simple cold frame, a box of boards or masonry blocks, and cover it with something translucent. I grew many of my first garden plants, including bulbs, in this way, though I now keep vulnerable seedlings in a solarium fitted with plant benches. Some growers in severe-winter regions grow seedlings in a basement under lights.

Others object, “It takes forever to get a flowering bulb from seed.” It can take many years for certain bulbs to flower, notably tulips, but most kinds can be raised to flowering size in four or five years, and some (*Allium* or *Crocus*, for instance) take only three. Some cyclamen, such as *C. hederifolium*, can even be flowered in a year. If you’re willing to plant a small tree or shrub and wait years for it to grow into a characterful specimen, you probably have the patience to raise a daffodil too.

The pros of growing bulbs from seed far outweigh the cons. If germination is reasonably good, it saves money, even when you invest $8 in a packet of 20 seeds and only 10 or 12 germinate. A “population” of seed-grown bulbs contains a number of different clones, genetically varied, so the grower can select the most vigorous or attractive, and the plants are much more likely to produce fertile
seed than are purchased bulbs, which may have been vegetatively propagated from a single clone. Many growers feel that bulbs grown from seed to maturity in one garden adapt better than mature bulbs brought in from elsewhere. Finally, home-grown seedlings are far less likely to be infected with the plant viruses and fungal or bacterial diseases rampant in commercial stock.

A “population” grown from seed is likely to display some color variation. You may get appealing hues like those seen in the photos of *Fritillaria pinardii*, *F. stenanthera*, and *Cyclamen pseudibericum* (pp. XX–XX). Seed saved from plants in cultivation may produce bee hybrids, such as that between *Fritillaria aurea* and *F. pinardii* (raised by Wim de Goede; p. XX) or several crosses between *F. purdyi* and *F. biflora* that arose in my own collection (p. XX), and these hybrids may have extra vigor as well as aesthetic interest.

Most of all, you can grow species from seed that are rarely if ever available as bulbs: western American *Calochortus* and *Brodiaea* from Ron Ratko’s Northwest Native Seeds or Sally Walker’s Southwest Seeds, collections from Central Asia and the Caucasus from a range of Czech specialists, or Mediterranean *Crocos*, *Iris* and *Narcissus* and Iranian *Fritillaria* from Jim and Jenny Archibald (now also offering John Watson and Anita Flores’s South American collections), along with special discoveries in the NARGS Seed Exchange and similar exchanges. Your own wild collections will be priceless souvenirs of your travels, like the *Alstroemeria umbellata* (p. XX) I grew from seeds I collected on a steep scree above an Andean canyon.

**General Procedures**

Different growers use different seed-sowing mixtures, but most of us stick with just one formula for almost all seeds. Mine consists of one part sieved peat, one part ground horticultural pumice, and two parts coarse, gritty sand, since these are materials readily available in my area. Many growers substitute Perlite for the pumice favored in the Pacific Northwest, and many like to use vermiculite in seed mixes. My mix works well for me but the pots are heavy to lift in the large flats I use; on the other hand, I think it retains moisture more evenly than mixes with artificial ingredients, since the pumice absorbs some water and releases it very slowly. As an alternative, John Lonsdale reports that BioComp BC5—a composted peanut hull-based compost available to growers in eastern North America—when mixed 50:50 with super-coarse Perlite, makes an excellent light, well-drained, moisture-retentive sowing and growing medium for all bulbs.

**When to sow.** A few kinds of bulbs have seeds with short viability in storage, and they are best sown as soon as possible after ripening, although some germination can be expected in most cases even if sowing is delayed but the seeds have been correctly stored. Examples include most bulbous *Corydalis*, *Fritillaria meleagris*, *F. camtschatensis* and possibly other northeast Asian species, some species of *Colchicum*, subtropical amaryllids such as *Zephyranthes* and *Habranthus*, and many of the ephemeral woodland geophytes. To predict short viability, consider
where the plant grows naturally: if seeds are likely to encounter moisture immediately after ripening and being disseminated, they may be short-lived, but if they ripen during a long dry season, they probably can withstand dry storage for months or even years. Art Guppy’s discussion of *Erythronium* in this issue is a perfect example of a genus in which species native to summer-rainfall areas have short-lived seeds while those from dry-summer regions have long-lived seeds.

The majority of geophytes (plants that spend part of their annual cycle as underground storage organs, such as bulbs, corms, and tubers) come from regions with moist winters and dry summers. Their seeds can be stored dry at room temperature until early fall and sown in cool, moist conditions at that time. The seeds should not be frozen, although some species tolerate freezing at this stage, but they should be kept cool—under 60° F/15° C—through the winter. I keep my ungerminated seed pots outdoors on a roofed deck, but when intermittent subfreezing temperatures are likely, I examine them frequently and place the seedlings that appear in a frost-free, cool solarium. A few kinds of bulbs can stand freezing when very young, but most cannot.

If you don’t get your seeds until after the New Year, I recommend sowing them right away. Some will experience a long enough chill to germinate in the current year, and others will remain dormant through an entire year and then germinate the following year. I have sown seeds received until April with success, but John Lonsdale writes, “If I get anything after the middle-end of February I refrigerate them until the fall. Here on the east coast anything that germinates in late spring doesn’t get enough time to build up a decent bulb before going dormant, and the seedlings are all too easily lost in the summer.” The difference in our experiences is probably due to the cooler temperatures, especially at night, during spring and summer in the Pacific Northwest where I live.

**How to sow.** I sow most bulb seeds on the surface of the seed soil mix, cover them with about 1 cm of fine granite grit, and press the surface down gently but firmly with a flat-bottomed pot. Large seeds, such as those of *Iris* species, can be covered with extra soil mix. Some small seeds, particularly *Crocus*, also benefit from deeper planting. Some growers plant flat seeds like those of *Lilium* and *Fritillaria* on their edges, but others think this is unnecessary.

**Care before germination.** Keep the pots slightly moist and unfrozen, in full light. Protect them from rodents; I find cheap “bird netting” adequate for this. Examine them frequently and move young seedlings into a well-protected place with strong light. Seeds of many bulbs, especially *Cyclamen*, fall-flowering *Crocus*, and western North Americans (notably *Brodiaea* and related genera) germinate in the fall. Pots containing ungerminated seed of dry-summer species can be allowed to dry out in summer, with watering resumed in fall. Gardening in Pennsylvania, John Lonsdale finds this very important on the east coast, where keeping bulb seeds moist in summer heat causes many to rot, especially crocuses and erythroniums.

**Care after germination.** This is a tricky period for the young bulbs. Provide as much sunlight as possible during winter, but shade them lightly in summer (in nature, they would probably be shaded by larger plants). Watch carefully for
aphids, which are especially attracted to Iris, Crocus, and other Iris family members. You can remove a few aphids by hand, but I use a systemic granular insecticide applied to the soil. I don't recommend spraying any product (even "organic" ones) on new seedlings. Another problem is damping off, especially in Calochortus; I don't know of any effective treatment, and the best way to avoid it is to grow your Calochortus seedlings as cold as possible without freezing them, and maintain as much air movement as possible. Naturally, protect the seedlings from slugs, snails, and other plant predators.

Apply a liquid fertilizer, diluted to about half the strength recommended by the manufacturer, to the seedlings two or three times during their growing season. Some growers add a small amount of superphosphate to the seed soil mix. Keep the seedlings moist but not soaking wet as long as they are growing strongly. Eventually they will approach their natural dormancy and begin to wither. Unless they're plants of constantly moist habitats (e.g., Fritillaria meleagris), reduce watering at this time and put the pots in a dry, shady position; I cover them with mesh-bottom flats and leave them on the covered deck, out of the sunlight. You can also cover trays of seedling pots with sheets of Styrofoam used as building insulation, which helps greatly to protect young bulbs from desiccation.

Moving on. Growers differ in when they transplant seedling bulbs into a new growing medium. I like to repot many kinds after their first year, but I leave Crocus and most Calochortus species in their seed pots for two years to develop corms large enough to handle easily. John Lonsdale prefers to leave all bulbs in seed pots for at least two or often three years. Let the seed pot's soil dry out so you can spot the young bulbs. Some will be obvious, others not. If you can't see any bulbs, don't despair; just put the soil back into the pot and set it with your ungerminated seed pots, and perhaps another cohort of seeds will sprout next year. When I find only a few bulbs in a seed pot, I top up their new pot with the soil from the seed pot, and often there are more seedlings to follow. I also fill in between the pots in my bulb frames with soil from harvested or completely failed seed pots, and sometimes this "last chance" produces plants.

To pot on the bulbs, fill your growing pot (because I plunge the pots in sand, I prefer clay but also use plastic mesh "aquatic" pots; John Lonsdale uses ordinary plastic pots) almost up to the intended surface level and distribute the little bulbs on it. They don't need to be very deep at this time—one inch (2.5 cm) below the surface is fine for most kinds, unless you find them at the bottom of the seed pot. Cover them with more of the soil mix you've chosen, and mulch with grit if you wish. I use a soil mix of 2 parts coarse, sharp sand, one part ground pumice, and one part forest topsoil. I don't mulch the tops of most pots because I have so many and replace the soil every other year, but it's probably better to do so.

John Lonsdale comments: "I use the BioComp:Perlite mix for everything, and always mulch with granite grit. I know we differ here—I always underpot to protect against overwatering, and find that bulbs like to be in a fairly confined space. Others use Styrofoam packing pellets with single or a few bulbs to bulk out the
pot.” I’ve tried the packing pellet strategy but found that it interferes with proper drainage and results in a disgusting mess during repotting, so don’t recommend it either.

It can be difficult to tell which end is up when dealing with seedling bulbs, but the good news is that in most cases it doesn’t matter; they’ll figure it out for themselves. Some, such as Narcissus and Erythronium, are vertically elongated and should be oriented properly. Others, such as Allium and Old World Fritillaria, make little round bulblets that seem to cope well with being sown at random. Crocus cormlets can also be “sown.” The roots will plunge downward and the stem upward, and in another year the bulb will be positioned normally.

Keep the young bulbs in pots until you feel they’re mature enough to go into the garden. If you’re putting them in troughs, they can go directly from seed pot to trough as long as they won’t be overwhelmed by other plants while tiny. I believe that bulbs grown in pots are best plunged in some well-draining medium, preferably sand. If, however, you’re growing them in solid plastic pots, plunging is not necessarily beneficial; most growers just stand them on a bench, perhaps on a layer of sand or gravel. For more information on managing bulbs at this stage, see my chapter on frames in the NARGS/Timber Press book Rock Garden Design and Construction.

Notes on Genera

Following are some observations on seed growing of individual genera of geophytes, including some dicots often included in bulb collections.

**Allium.** Almost all are easy from seed, which is available in great quantity and variety through exchanges. Most germinate within 3 months from fall to winter planting. The tiniest species, many from the American West, should be left in seed pots 2 years, but most can be identified and replanted during their first dormancy. Some species are summer-growers (e.g. A. cernuum, A. cyaneum) and should be grown like herbaceous perennials rather than summer-dormant bulbs. Many species flower in 3 years from sowing.

**Aldstroemeria.** Not a bulb, but often grown in collections of geophytes. The seeds appear to benefit from a period of warm dry storage before sowing. Germination occurs in cool, moist conditions, usually within one year. Seedlings can be transplanted carefully when they have 4 leaves. Don’t leave multiple seedlings in a single pot for too long, since the brittle roots will be difficult to disentangle. (Photo, p. 259.)

**Anemone.** Species with “cottony” seeds coated in fluff tend to remain viable in storage, but those with smooth seeds usually do not. Germination of stored seed can be erratic, with seedlings appearing sometimes after 3 years, so keep the pots. Do not dry out the young seedlings completely after they go dormant. They can be potted on while in new growth the second year after germination, or, if the seed pot contains only one or two plants (as often happens), simply remove the
entire soil mass into a larger pot of growing mix, or a rock garden site, while the
plant is dormant, setting it at about the same level in the soil.

_Arum._ Plant the large seeds well down in the pot. Germination can be erratic
over several years. The young tubers are easily identified and should be potted on
after one year, because they will enlarge rapidly. The top of the tuber has a little,
folded-over "topknot."

_Bellevalia._ Easy from seed, flowering in 3 years. The lovely turquoise _B. fornic-
ulata_ should not be dried out completely at any time of year. The young bulbs are
usually glossy white and should be planted with the narrow end upward.

_Biarum._ See _Arum._ Germination in this genus seems better than in _Arum_, and
flowering can occur in 4 years from sowing.

_Brodiaea._ Germinates at a high rate within 3 to 5 months of fall planting,
often within weeks if the seeds have been stored for any time. Seeds remain viable
for many years in dry storage, whether or not temperature-controlled. Small
brown bulblets are readily identifiable. Flowering takes 3 to 4 years from sowing.
Give large species plenty of depth for growing.

_Calochortus._ Seeds remain viable a long time in dry storage. Most species ger-
minate well within 3–5 months. Sow thinly to help prevent damping off, a com-
mon problem in this genus, and keep the seedlings as cool as possible without
freezing them. Most species, other than the largest and most vigorous, are best
left in the seed pot for 2–3 years. The bulblets are brown, fibrous-appearing, and
much elongated, and should be planted about three times their length deep in
the soil. Flowering typically takes 4 to 5 years, sometimes less in _C. venustus_ and
its close relatives.

_Cbionodoxa._ Germination is fairly high, with most bulbs flowering in 3 years.

_Colchicum._ Plant seed fresh if possible. Stored seed germinates very erratically,
if at all; keep seed pots up to 5 years. Germination appears to be environmentally
triggered, as typically several species from several years’ sowing will germinate
within days of one another, often in a midwinter warm spell. The seeds tend to
rise to the surface, so plant them rather deep with plenty of grit top-dressing. Small
species can flower in 4 years from germination, larger ones perhaps taking longer.
Growing colchicums from seed is only for the patient and expense-tolerant.

_Corydalis._ Fresh seed germinates far better than stored seed in most species, and
seeds can be damaged by rough handling in the mail, so this is another gamble.
Nevertheless, a small number of seeds, even from stored stock, may germinate. The
seed pots should not be dried out severely, even in the case of dry-summer dwellers,
and plants should be left in the seed pots for 2 years.

_Crocus._ Germinates fairly well, usually at the time of year the species would
normally begin foliage growth. Plant the seeds deeper than you would normally
place such small seeds, because a radicle (first root) emerges first and can push up
above the surface if the seed (which is on the tip of the radicle) is placed too shal-
lowly. The leaf emerges a little later, but in the same season. The seedling corms
are mostly very small. Flowering takes 3 to 4 years.

_Cyclamen._ Fresh seed germinates much better than stored seed, but enough
germination can be obtained from stored seed to make it worth a try. Germina-
Tubers are identifiable after one year but can be left in the seed pot two or three years to advantage, unless very crowded. Do not let the dormant tubers dry out severely, but don't keep them too moist either when it is hot, and keep them in the shade. John Lonsdale, who has an extensive collection of this genus, covers dormant pots of all Cyclamen species except graecum, persicum and rothsianum with Styrofoam sheets.

**Dichelostemma.** See Brodiaea.

**Erythronium.** See the feature article in this issue for detailed information on seed viability. Eurasian and eastern American species’ seed should be planted fresh; western American species’ seed remains viable in dry storage for at least one year. Germination of the latter from fall planting is high, and bulblets can be moved on during their first dormancy. They are elongated, and the larger end, usually lighter in color, is the bottom. No species should be “baked.” Some flower in 3 years, most in 4 to 5.

**Fritillaria.** A few species (F. meleagris, F. camtschaticensis, and possibly other East Asian natives) have short seed viability and must be planted fresh and not allowed to dry out completely at any time. Other species remain viable in dry storage for one year, with germination rates diminishing greatly thereafter. Some growers plant the seeds “on edge,” but I don’t find this necessary. Germination of Old World species usually occurs 3–5 months after sowing, but North American species planted in fall often germinate almost immediately. Bulblets can be left in the seed pots for 2 years, but they are easily identified unless you use perlite in the mix (they look like slightly irregular pearls). Fertilizing is especially beneficial in this genus, but use a dilute strength. (Photos, p. 258.)

**Galanthus.** Snowdrop seeds apparently do not remain viable in storage and should be planted immediately after ripening. After germination, do not allow the pots to dry out completely, and keep them in a cool site even while dormant. Keep in seed pots for 2 years.

**Gladiolus.** I grow mostly the hardy Eurasian species, very easy from seed, germinating copiously and flowering in 3–4 years. The small, elongated, brown first-year bulblets are hard to identify, so leave them in the seed pots 2 years, providing ample fertilizer.

**Gymnospermium.** This tuberous member of the Podophyllaceae is popular with bulb collectors and can be increased only via seeds. Plant the large seeds at a good depth in a well-drained soil mix. The young tubers are light brown and easily identified. This is a fairly large plant, so move them on to a pot with plenty of depth after one year. The seeds have elaiosomes eaten by ants, and volunteers often appear some distance from the parent plants.

**Iris.** Growing irises of the Reticulata section from seed is a good choice, because they germinate readily, reach flowering size relatively quickly, and can thus be freed of the prevalent Ink Spot disease (as long as you keep them away from commercial Reticulata bulbs). First-year bulblets are quite small. Also popular with bulb enthusiasts are members of the Scorpiris (Juno) section. The large seeds should be sown deeply and germinate erratically over several years. Handle the young dormant plants very carefully so as not to damage the developing storage roots.
Leucojum. Many former members of this genus have been moved to Acis, and it is in the latter genus that we find those most likely to have storage-tolerant seeds; L. vernum and L. aestivale should be sown fresh. The Acis species (including the much-grown former L. autumnale) tolerate dry dormancy and germinate readily. Seedlings are small.

Lilium. The growing requirements of this huge genus are too varied to condense here. For details see Edward McRae’s book Lilies: A Guide for Growers and Collectors (Timber Press, 1998). Because viruses are such a severe problem in lilies, growing species from seed is strongly recommended.

Muscari. Most are very easy from seed, forming good-sized first-year bulblets, usually glossy white with an obvious enlarged base.

Narcissus. A top choice for seed growers. Seed germinates readily and produces easily identified brown, elongated bulblets the first year. (John Lonsdale comments, “Elongated bulbs are often a sign of too-shallow planting—plant them deeper and they’ll become round.”) Don’t dry them out completely. Smaller species can flower the third year. Garden-collected seed is likely to produce hybrids unless the stock is carefully hand-pollinated.

Ornithogalum. Another easy genus that can be moved on during its first dormancy.

Scilla. Most germinate readily the first year and can be moved after one season.

Sternbergia. Import restrictions make this a genus needing seed propagation. Germination can be erratic, suggesting that seeds be planted fresh even though sternbergias come from dry-summer regions. The brown bulblets develop quickly.

Triteleia. See Brodiaea.

Tulipa. Germination is usually moderately successful, but you may wait many years for flowers. A few species (e.g., T. cretica, T. sylvestris) flower when fairly young. Move the bulblets on to pots with plenty of depth. Another genus where widespread virus disease in commercial stocks makes seed growing desirable.

Acknowledgments

I would like to thank John Lonsdale for reading and commenting on the first draft of this article; note that our methods diverge in some respects, and the recommendations, unless attributed to him, reflect my own practice. Sincere thanks are also due to the many growers and collectors whose work has made my own efforts possible, especially John Andrews, Jim and Jenny Archibald, Alan Bradshaw, Phyllis Gustafson, Josef Halda, Josef Jurasek, Brian Mathew, Mojmir Pavelka, Vlastimil Pilous, Ron Ratko, Jim and Georgie Robinett, Janis Ruksans, Loren Russell, Michael Salmon, Sally Walker, John Watson and Anita Flores, and the contributors to Andrew Osyany’s “Karmic Exotix” seed list.

Jane McGary, editor of this publication, gardens in the foothills of the Cascade Mountains southeast of Portland, Oregon. To receive her annual surplus bulb sale list, write to janemcgary@earthlink.net

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In the fall 2006 issue of the Rock Garden Quarterly, I asked you what you would do with just two capsules of Omphalogramma forrestii seed, at risk from plant diggers and grazing yaks ("Turning the Chinese Grab Bag Inside-Out," p. 287). When faced with this dilemma we had to make a decision—fast. We debated the pros and cons of various choices for a few minutes, and then made our decision.

In my original article I asked readers to let me know what they would have done. Thanks to those who responded—although my overwhelming impression is that few care. Or are you just too busy? Anyway, five of the six who wrote said that they would take some seed to grow themselves—between 10% and half of the total number of seeds that were there—while the sixth said that, in general, we should grow rare plants outside China. Two also said that we should encourage the cultivation of alpine plants in China, although our experience is that this is an uphill struggle, as there is no custom of growing alpines there in private gardens. So the idea of taking some seed to a local commercial nursery that could eventually sell the plants was, unfortunately, not really practical.

Three of the six respondents also said that they would sow the seeds that they did not take, in suitable sites in the vicinity. One would leave one of the two capsules to the yaks, and the other two did not specify what they would do about seeds that were not collected.

Not too bad! I think most would have approved of what our field group in fact elected to do. The group consisted of both Chinese and European scientists and horticulturalists, and included a member of the government of the province. We decided:

• to leave one capsule as it was, to take its chance with the yaks;
• to take half of the seeds (about 30) from the second capsule, and sow them immediately in the small area of suitable habitat, selecting places where shrubs would restrict yak access;
• to take half of the remaining seeds, to be sown in a botanic garden nursery in the Chinese mountains; and
to take the remaining 15 seeds to be sown in Scotland, with the condition that seed from any plants that were raised successfully would be returned to China, to restock the original area.

That was our choice, on the spur of the moment. A year later there were four plants growing in our nursery but, sadly, there had been no germination in the Chinese nursery. It will probably be 2008 before there are any flowers, so we will have to take great care to bring the plants safely through two winters. Meanwhile, there is some good news. Members of a botanical expedition in 2007 stumbled on this population of Omphalogramma forrestii, while watching birds! There were about 20 plants in flower (photo, p. 260), so the small plants seen the previous year had managed to grow to maturity. Whether the yaks got to them before their seed ripened we do not know, but there is some hope.

There are no simple, “correct” answers to the questions I asked, but I hope that I have stimulated thought. There are moral, ethical, and legal issues, as well as pragmatism, and there are no easy answers. We should hesitate to lay down the law for others. But I hope that we will all think about the consequences of our actions, and be aware that in our enthusiasm to see, grow, and enjoy wonderful mountain plants, we could be contributing to their demise.

David Rankin is Professor of Chemistry at the University of Edinburgh in Scotland. He and his wife, Sheila, operate Kevock Garden Plants, a nursery specializing in alpine and rock garden species.

Reviewed by Brent Hine, Vancouver, British Columbia

Living in the climate of the Pacific Northwest coast (= rainforest), I am seriously challenged in my attempts to grow plants that are firmly alpine instead of the sometimes more elementary rock and montane plants. As well, the alpine garden I steward—at the University of British Columbia Botanical Garden in Vancouver—is sited 700 feet from and 300 feet above the Pacific Ocean—hardly in the alpine zone! However, this book offers alpine and rock gardeners everywhere the means to enlarge their understanding of fundamental aspects of alpine plants, which in turn upgrades the skill set required to manage them more effectively.

By way of introduction, it is a stimulating read. Appropriate perspective is applied early in the preface, where John Good presents an attractive nugget: "While about 3 percent of the world’s land surface lies above or beyond the timber line approximately 6 percent of the world's flowering plants (c. 12,000 species in 2000 genera and 100 families) occur there." Wow! There is a wealth of alpine material to appeal to our sense of challenge—but how can it be better grown? Proceeding with an overview of the alpine and arctic environments, we are informed that alpine plants inhabit the most dynamic ecosystem on Earth. The alpine zone we happily wander during summer, when benign conditions prevail. Year after year alpines in the natural environment persevere despite extremes of temperature, radiation, and precipitation and do so in soil conditions that often provide paltry nutrition. The effects of snow cover are considered. How do plants under snow manage to photosynthesize? (With great difficulty.) As little snow depth as one foot (30 cm) reduces light transmission to zero. As for benefits, besides insulation snow delivers valuable soluble nutrients to plants during the spring melt.

Scattered generously through the book are references to scientific studies consulted, and listed in the bibliography. The process of hardening off is exam-
How do plants deal with this? Some (e.g. ridge plants) are not covered by snow all winter. I need only think of my coastal site during winter—virtually snowless, rain-soaked and heavily overcast. These are extreme conditions even for plants already extreme-adapted. Freeze-thaw cycles and challenges of roots and shoots contending with them are also discussed.

David Millward scrutinizes geology and soils. He begins by recognizing that every serious alpine gardener needs a good working knowledge of rock types. Tables provide useful field identification guides to the three main families: igneous, sedimentary, and metamorphic. The discussion of various rock landscapes contains practical applications for observations on future mountain journeys. He adheres to the same basic theme, to provide the reader with fundamental knowledge leading to cultural improvement of their alpine treasures.

Further along, Good introduces essential elements of nutrition and reproduction. Reproduction is the basis of all life, and alpines do it in various intriguing ways. Some of them simply eliminate pollination, accomplishing the task via apomixis or vivipary (definitions appear in a glossary), thus conserving vital energy. Finally, two chapters discuss “Factors influencing the origins and present distributions of arctic and alpine plants” and “Impact of global climate change on alpine plants.”

A caveat at the book’s end offers a note of hope to those passionately involved with plants: “Climate change is sure to further test the ingenuity and skill of alpine gardeners. But after all, overcoming challenges has always been a central characteristic of the true alpine grower.” Well said, and well done.

This book is not long and is easily read over a few weekends. Liberal use of images and diagrams also delivers a reasonable amount of information for an introductory work. Overall, it offers an education that aids the ongoing struggle to engage with this formidable yet rewarding set of plants. It helps us to enjoy them on their terms, while they inhabit our gardens, which is all anyone can ask. For those craving deeper insight, see the review of Christian Korner’s Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems (Rock Garden Quarterly 59(2):136–37, Spring 2001)


Reviewed by Michelle Jones Ham, Rushville, New York

Cliff Ecology is not strictly a collegiate manual. While it is a detailed ecological, geological, and geomorphological text, it’s descriptive enough that I only had to refer to my Horticultural Dictionary a few times. This book should fascinate all rock gardeners because it discusses the biodiversity of ecosystems found on inland cliffs, maritime cliffs, mountainous cliffs, and human-made cliffs. It is a book that explores all the fascinating similarities and differences in both flora and fauna endemic to cliff systems worldwide.
The authors take pride in the fact that this is the first book to study what they have defined as “true” cliff ecosystems. Within their scope, a cliff is a single unit with a cliff edge (flat surface leading up to a cliff face), cliff face with greater than an 80° angle or an undercut with up to a 180° angle, and a talus base—all of which can support the same plants and animals. It is their belief that because cliffs don’t fit the conceptual model of ecosystem habitats, cliffs have been virtually overlooked by ecological studies. Possible reasons mentioned for this oversight might be that cliffs are dangerous, requiring climbing equipment to study and researchers who don’t suffer from vertigo.

The book clearly outlines the patterns of cliff ecosystems: geology, heterogeneity, weathering and erosion, hydrology, incident radiation, moisture, wind, temperature, and the impacts each has on a cliff’s physical environment. It goes on to discuss the evolutionary effects that each of these factors have on the development of species composition in cliff ecosystems. The authors suggest that cliff ecology is best studied as “ecology of place,” not ecology of species.

Of particular interest to alpine gardeners might be the finding that in most cliff systems 35 to 40 percent of endemic alpine taxa live in vertical crevices on steep slopes and rock faces; that can climb as high as 66 percent in some areas. However, one must not assume that because these are plants living on a cliff, they require desiccated conditions. Because cliff systems may include flat outcroppings, sheer faces, cracks and crevices, caves, moist seeps, and talus, individual cliffs may support different microhabitats within centimeters of each other. One microhabitat might host desert plants, the next wetland species.

Following the analogy of holding a wet sponge by one corner and watching the water drip from the bottom, the authors found cliff conditions to be the driest at the upper cliff edge, dry to moist on the cliff faces with microhabitats throughout the face, and moist to moraine conditions within the talus. Further, they found that plants that are the rarest and most difficult to grow are longest-lived in the face of a cliff. Such plants do proliferate in the talus but are not as long-lived there. It seems that the rarest gems need the stability of the cliff face to prolong life, while the instability of the talus shortens their lifespan. This may explain why I have watched rare plants wither within a few years in my scree gardens or perish in my newly constructed, unstable trough communities.

In addition to the flora and fauna studies, the authors also take a brief look at human interaction with cliff systems. Early humans may have used cliff overhangs and caves for shelter, but the human fascination with cliffs has endured long beyond this functional use. Each chapter of this book is introduced with a vintage postage stamp depicting cliffs around the world. Proving a modern-day fascination with cliffs, a study of four major magazines over a one-year period found cliffs depicted in the foreground of over 25 percent of advertisements.

While I may have highlighted this particular rock gardener’s interest in the book, I highly recommend it for anyone interested in alpine gardening, geological chronology, climatology, or biodiversity. The authors encourage future research on cliff environments to address the gaps in our current understanding of previously ignored “places.”
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Classes:

Class 1: Portrait of a plant in the wild. Image should be centered on the plant, but extreme close-ups are less desirable than photos showing the entire plant.
Class 2: Natural scene featuring wild plants. The plants should be clearly visible, but this is not a “portrait”; that is, a broad view of the habitat should be shown.

Class 3: Portrait of a plant in cultivation. Extreme close-ups are less desirable than views of the whole plant. Plants illustrated should be “suitable for the rock garden” in the broadest sense—small in scale. Photos of potted specimens should be artistically composed.

Class 4: Rock garden scene, showing both landscape elements and plants. Vignettes of small areas are often more appealing than broad views, but the images should not be individual “portraits.”

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